BIOGEOMORPHIC HIERARCHIES IN CORAL-REEF ECOSYSTEMS: REEF GEOMETRY AND FISH POPULATIONS

By

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Abstract of Dissertation Presented to the Graduate School
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BIOGEOMORPHIC HIERARCHIES IN CORAL-REEF ECOSYSTEMS: REEF GEOMETRY AND FISH POPULATIONS

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This study examines how the physical structure of shallow marine substrata affect the size and body mass of fishes occupying these substrata. The purpose was to test two separate but related hypotheses which state that the geometry of substrate types shapes the morphology of fishes (the Textural-Discontinuity Hypothesis) by limiting the quantity and sizes of available shelter spaces in coral-reef environments (the Limited Shelter Hypothesis). Using data collected by the National Marine Fisheries Service for 3693 sample sites in the Florida Reef Tract, statistical profiles were developed and compared for the community characteristics and size structure of coral-reef fish populations occupying substrate types composed of homogeneous mixtures of differing proportions of coral, rock, rubble, grass and sand. Results indicate that significant intersubstrate differences occur in size and body-mass distributions, which are coincident with changes in geometric textures. Structures of greater complexity, such as corals, entrain more fish body mass in larger-sized body-mass clusters than do less-complex substrata of similar spatial extent. As specific textural frequencies are removed from the reefscape, so too are specific size clusters of fishes. Fishes in the 10-20 cm size range, which are dominate in coral bottom covers, quickly disappear as the substratum changes to rock, rubble, grass and sand, which are dominated by progressively smaller-sized fish populations. Cumulative size curves of species and abundance computed from multiple random samples in different reef zones display relatively narrow size ranges whose dominate frequencies uniquely define specific substrate types. While mean numbers of species and abundance do not differ significantly between aggregate coral, rock and rubble samples having similar bottom-cover proportions, these variables do show significant increases across surface-area gradients. Within substrate types, fish size also increases with surface area, suggesting that both the size and absolute numbers of shelter spaces increase directly with structure size. Similar intersubstrate size-structure shifts are found in all reef zones, seasons, trophic classes and dominant as well as non-dominant species. These results suggest that substrate types may provide an important variable in modeling fish biomass in coral-reef ecosystems.

CHAPTER 1
INTRODUCTION AND LITERATURE REVIEW

Coral reefs are biogenic aggregations of carbonate-secreting organisms whose high biological productivity and complex morphology serve as focal points for the concentration of life in the tropical oceans. A vast literature has accumulated on topics concerning both the physical and biologic structure of these ecosystems and the processes that shape them. Biogeomorphic structures and processes have been particularly well studied. Intermediate and macroscale zonation patterns are well documented from reef structures in many areas of the world and have been shown to recur with some regularity given similar sets of environmental conditions. At microscales, taxonomies of reef organisms are well developed and certain organizational patterns in biologic productivity and community structure have been identified at intermediate scales. Yet, despite the advances in our knowledge of ecosystem components and functions, the fundamental dynamics of organizational forces that shape these assemblages of biotic and abiotic elements into functioning ecological structures is still poorly understood. Questions concerning spatial and temporal differences in abundance, diversity and community structure of organisms within coral-reef landscapes have continually defied systematic efforts to model them.

Various authors have suggested that the physical architecture of the environment may shape the morphology and community structure of the biota which develop in any geographic location. The origin of this concept has been attributed to R.H. MacArthur

(Holling, 1992) and has been enhanced by conceptual developments in hierarchy theory (Simon, 1973; Allen and Starr, 1982; Allen and Hoekstra, 1991; O'Neill et al., 1986, 1991) and fractal geometry (Mandelbrot, 1982) which suggest that natural phenomena may be organized into discrete clusters or assemblages of forms and processes which may be self-similar or discontinuous across various spatial and temporal scales. Holling (1992) has suggested that a small set of biotic and abiotic processes structure ecosystems across scales in time and space, establishing a small number of dominant temporal and spatial frequencies that entrain other processes and lifeforms. He states that such 'keystone' processes form discontinuous interacting clusters of biotic and abiotic relationships, which are hierarchically structured and nested within each other across scales. Each cluster should have its own architecture of distinct object sizes and interobject distances (Holling, 1995). In this view, the morphology of animals is shaped by the physical and biotic geometry of the landscapes that they occupy. The size and magnitude of animal body-mass concentrations will depend upon the extent to which particular, scale-specific textural frequencies are developed in the landscape architecture. Thus the distributions of animal body sizes and mass may serve as a bioassay of ecosystem structure (Holling, 1992) and provide a mechanism for modeling the productivity and structural characteristics of organisms within such systems.

The primary purpose of this work is to test the proposition that the community characteristics of coral-reef fish populations, specifically their size, mass and abundance, are organized into specific patterns which reflect the physical geometry of coral-reef substrata. If such characteristics can be linked to the structural properties (textures) of reef landscapes, then it may be possible to utilize substrate inventories or estimates as variables for modeling fish productivity in reefscapes. Similarly, the identification of such relationships may make it possible to predict impacts on reef fish communities which are due to human or natural impacts on the physical landscapes which they occupy. Such knowledge could prove extremely useful in the management of coral reefs and adjacent ecosystems.

This research is particularly relevant in light of the increasing consensus that human activities are adversely affecting reef-system structures over large areas of the world. Water quality changes associated with coastal development and land use practices have been shown to affect the physical structure of coral reefs through their impacts on the structuring organisms (Dodge et al., 1974; Dodge and Vaisnys, 1977; Brown and Howard, 1985; Grigg and Dollar, 1990; Ogden and Ogden, 1993). Reef systems appear to be in rapid decline in most areas where they are in close proximity to large human populations (Smith and Ogden, 1993). Wilkinson et al. (1993) conclude that Southeast Asian coral reefs are being degraded at a rate that approximates that of population growth. Similarly, widespread destructive fishing practices using dynamite and sodium cyanide dramatically alter reef structure (Saila et al., 1993; Johannes and Riepen, 1995). Overexploitation of dominant predator fishes has also been shown to affect reef structure and reef-fish productivity adversely (McClanahan, 1990, 1995). If the biophysical characteristics of reef-fish populations are closely associated with those of the reef and its structuring organisms, then serious changes in the characteristics of reef fisheries can be expected wherever the structuring organisms are depleted or the existing structure destroyed.

Coral-Reef Ecology

Coral reefs are wave-resistant, carbonate structures of biogenic marine origin, which form in the warm, shallow, transparent and well-illuminated oligotrophic waters of the worlds' tropical oceans (Achituv and Dubinsky, 1990). They are composed of the shells or skeletons of hermatypic or reef-building organisms; the most important of which are corals and coraline algae. The reef structure is built over long periods by successive generations of such organisms, which form a thin veneer on the reef's outer surface and secrete calcium carbonate as a part of their lifecycle. Such ecosystems have existed for over 450 million years (Copper, 1974; Wells and Hanna, 1992) and currently cover some two million square kilometers of the tropical oceans (Achituv and Dubinsky, 1990).

Reef Framework: Composition and Genesis

Calcifying organisms within coral reefs include both plants and animals. Many have developed an endosymbiotic relationship with unicellular plants, often called zooxanthellae (Barnes and Chalker, 1990). The growth and maintenance of coral-reef frameworks are dependent on rapid calcification, which has been linked to light through the metabolic process of photosynthesis. This is accomplished by the zooxanthellae, which live in the tissues of the hermatypic hosts and provide most of the carbon used in skeletal construction (Hopley, 1982; Barnes and Chalker, 1990). Chalker (1983) notes that about half of all carbon fixed by the zooxanthellae is translocated to the animal host's tissues where some proportion is used for skeletal construction.

The framework of the coral-reef structure is primarily attributable to the skeleton-building capacities of the massive corals (Stoddart, 1969). Thus, the coral-alga assemblage, which provides the mechanism for rapid calcification, is considered by some to be the primary structuring process in such ecosystems. Scleractinian corals build a loose, open structure, which is infilled and consolidated by other carbonate-secreting organisms. Its rugged characteristics reflect the multitude of forms which can be assumed by these colonial organisms (Hopley, 1982). The reef framework is reinforced by encrusting coraline algae, particularly on the windward side of the reef (Hopley, 1982). Inner cavities are filled by bryozoans which play an important role in consolidating frail coral foundations (Hopley, 1982). Skeletal sediments and other calcifying organisms further reinforce the overall structure. These include foraminifera, sponges, mollusks and echinoderms (Chalker, 1983).

Coral reefs exist because calcium carbonate deposition exceeds rates of mechanical and bio-erosion. Growth rates have been shown to average about 10-12 mm $yr.^{-1}$ for massive coral species and 100 mm $yr.^{-1}$ for branching species (Buddemeier and Kinzie, 1976). When expressed in terms of solid radius expansion, the rates between forms are nearly equal (Maragos 1972, as cited in Hopley, 1982). These averages have large variances, which reflect different growth environments and biotic assemblages across the reef. Kinsie (1983) points out that typical reef perimeter calcification rates are in the order of 4 kg $CaCO_3$ m^{-2} $yr.^{-1}$ while lagoonal rates ranged from 0.5 to 1.0 kg $CaCO_3$ m^{-2} $yr.^{-1}$. Such differences reflect the differential concentration of living corals along the high-energy reef margins while backreef areas are dominated by sediments with variable alga cover (Figure 1.1).

Although the primary structuring organisms (the corals) are animals, coral reefs may be composed of a greater fraction of plants. Wanders (1976) found that, on average, the substrate under one square meter of sea surface on a shallow reef in the Netherlands Antilles contained 2.1 m^2 of coraline algae and 0.8 m^2 of fleshy algae as compared to 2.1 m^2 of coral polyp tissues. This calculation did not include any measure of symbiotic algae or water-column phytoplankton. At Eniwetok atoll, Odum and Odum (1955) found that the ratio of all algae to other marine life forms was five-to-one as measured by dry weight. Other studies have shown

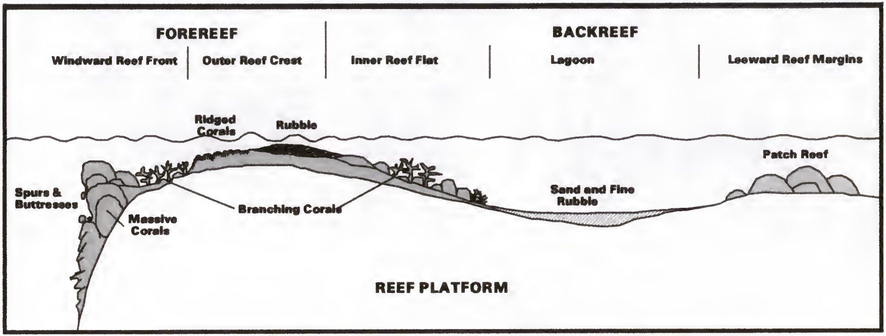

Figure 1.1. Reef-Platform Cross Section. Reef zones according to Hopley (1982).

that aragonite deposits of the calcareous green algae, Halimeda, may form up to 80 percent of the sand which fills the areas between corals in certain parts of the reef (Berner, 1990). Given such data, it has been suggested by some that ‘coral reefs’ should in fact be called ‘biotic reefs’ or ‘alga reefs’ (Berner, 1990). Stoddart (1969) notes that the term ‘coral reef’ is retained because of the primary importance of the massive corals in framework construction.

Primary Production and Nutrient Cycling

Coral-reef ecosystems have evolved in the oligotrophic (nutrient-poor) environments of the tropical oceans but are considered by many to be one of the most highly productive ecosystems on the planet. They support a huge diversity of plant and animal life which has been ranked second only to rainforests (Wells and Hanna, 1992; Sorokin, 1990a). Gross autotrophic production on the reef ranges from 5 to 20 g C m^{-2} d^{-1} with an average of about 8 g C m^{-2} d^{-1}, versus 0.05 to 0.3 g C m^{-2} d^{-1} in the ocean (Sorokin, 1990b). Thus, gross biological productivity per square meter may be 50 to 100 times higher than in the surrounding tropical oceans. The net productivity of coral reefs may, however, be much smaller, perhaps only 2 percent of average gross production (Smith, 1988). Carter (1988) notes that coral reefs average two to three times the net production of any other coastal ecosystem.

Although most reef systems appear to be in autotrophic balance, production is heavily concentrated along the high-energy margins (Figure 1.1). Excess organic production along this perimeter is transported leeward to less productive interior zones of the reef (Kinsie, 1983). Production variances show the same spatial distributions as those for carbonate deposition with measurements ranging from 20 g C m^{-2} d^{-1} along the outer reef slopes and crest to 5-10 g C m^{-2} d^{-1} on the reef flat to 1 g C m^{-2} d^{-1} on bare sand and rubble bottoms (Kinsie, 1983).

The secret to this high productivity is extremely complex, but appears to involve several interconnected processes: primary production through photosynthesis; a relatively closed system of nutrient cycling between many reef organisms; and the highly adapted capabilities of certain reef organisms to import basic nutrients to the system through the biofiltering of nutrient-poor oceanic waters. This combination provides for a positive balance of nutrients in an otherwise nutrient-deficient setting (Erez, 1990; Sorokin, 1990b).

Photosynthesis appears to provide most of the organic carbon and much of the oxygen required by reef organisms for growth and respiration (Barnes and Chalker, 1990; Hopley, 1982). Autotrophic benthic communities form dense populations on the reef with a high potential for photosynthesis. These communities include macrophytes, sea grasses, periphyton, microphytobenthos, reef symbionts and sometimes phytoplankton (Sorokin, 1990b). The symbiotic algae, which live in the tissues of corals, foraminifera, sponges, and certain mollusks and tunicates, are considered by some to be the major primary producers of the reef system (Hopley, 1982; Erez, 1990). Others suggest that highly productive turf algae that are intensively grazed by fish and invertebrates may represent the largest component of primary production (Lewis, 1977; Larkum, 1983).

The reef ecosystem needs to maintain a positive balance of nutrients, primarily nitrogen and phosphorus, in order to support this high autotrophic production. This is accomplished through a relatively tight system of nutrient cycling between reef symbionts, nitrogen fixation by bacteria, and direct uptake from sea water passing over the reef (Sorokin, 1990b; Erez, 1990). Nutrient cycling is typified by the symbiotic relationship between zooxanthellae and corals where the primary products of the autotrophic algae (reduced organic carbon and oxygen) are utilized by the host which, in turn, passes back waste products from its respiration (carbon dioxide) and digestion (ammonium and phosphate). In this way, nitrogen and phosphorus are efficiently recycled between decomposer heterotrophic cells and autotrophic plant cells within the same body (Sorokin, 1990b).

This symbiotic recycling is not 100 percent efficient however, and certain amounts of nutrients are exported from the system. In addition, large amounts of nutrients are lost through the excretion of ammonium and phosphate by higher trophic level consumers such as fish, mollusks and echinoids that feed on the primary producers and each other. Some of these are reused by algae and corals in the immediate vicinity, but much is carried away by tides, waves and currents (Erez, 1990). These nutrients are replaced by a combination of nitrogen-fixing bacteria and a dense population of periphyton microflora and other predatory and filter-feeding reef fauna which serve as a giant natural biofilter with an enormous surface area through which the dissolved and suspended organic matter of the oceans is strained as it moves across the reef (Sorokin, 1990b; Erez, 1990). Predatory fauna includes corals that actively feed on zooplankton, which may be important for the nitrogen and phosphorus, it supplies. In such ways, a positive nutrient balance is maintained within the ecosystem.

Secondary Production

Coral reefs serve as focal points for the concentration of higher trophic level lifeforms in the tropical oceans. Individual and symbiotic reef organisms create the structure and primary production that provides habitat and food for a host of heterotrophic consumers. These include a variety of invertebrate and vertebrate marine lifeforms which form feeding groups on the reef that specialize on various food sources. Such sources include: plankton, algae, sea grasses, particulate and dissolved organic matter, photosynthate from symbiotic algae, mucus secretions, micro-organisms, corals, carrion, and various other sedentary or motile animal populations (Glynn, 1990).

Production associated with these communities of secondary producers is likely very significant and related somehow to primary production, but studies in this area have been limited. The few existing production estimates concentrate primarily on reef fish. Montgomery (1990) notes that fish contribute large amounts of biomass to coral-reef ecosystems and attain large standing crops with estimates ranging from 350 to 1950 kg per hectare (Goldman and Talbot, 1976; Mensaveta et al., 1986). Production estimates of roughly 35 percent of the standing crop per year were developed separately for reefs in Bermuda and Hawaii (Bardach, 1959; Polovina, 1984). Since a large number of fish feed extensively on invertebrates (micro- and macro-invertivores), it seems likely that production figures for these organisms would also be high. In their pioneering study at Eniwetok atoll, Odum and Odum (1955) estimated the biomass of producers to be 703 grams per square meter as compared to 132 grams of primary consumers and 11 grams of secondary consumers.

Coral-Reef Geomorphology

The literature suggests that the spatial distribution and geomorphology of coral-reef ecosystems reflect the dynamic interplay of geophysical and biotic forces operating across a wide range of spatial and temporal scales. At very small scales (large areas), geophysical processes dominate, setting the environmental parameters and shaping the underlying geomorphologic interfaces to which corals and their assemblages of associated organisms have adapted. At very large scales (small areas), the hermatypic biota are the primary structuring forces, actively modifying their growth environment and shaping the microscale texture of tropical reef landscapes. In between, biotic and geophysical processes overlap, creating form and texture at intermediate scales (Stoddart, 1969; Hopley, 1982; Guilcher, 1988; Holling, 1992). The terms large and small-scale are used here in a manner which are consistent with the geographic literature and refer to the fraction resulting from the ratio of map to ground distance. In this sense 1:1,000,000 would be small scale and reference a large area. Conversely, large scale would reference a small area.

Macroscale Morphology and Processes

At very small scales, the geomorphology and spatial distribution of coral reefs reflect the structure of the tropical sea floor and various geologic, climatic and physical processes operating at scales that range from tens to thousands of kilometers. Here, successive generations of hermatypic organisms have built extensive linear structures on shallow geomorphic platforms of the open oceans and fringing continental or island landmasses. At such scales, reef forms and their spatial distributions reflect the influences of very slow, aerially extensive geologic and climatic processes that shape their growth environment by means of tectonic movement, currents and the rise or fall of sea levels. Such macroscale morphology is clearly shown in the linear reef patterns that have developed along the seaward edges of the Florida Keys (Figure 1.2A).

At the coarsest resolution, such processes grade from planetary to continental in scale. Differential solar heating in combination with the placement and movement of continents as well as climatic fluctuations control the distribution of environments that are conducive to coral growth. Solar radiation provides the energy that heats tropical water columns. Geotectonic forces move and redistribute the margins of continental landmasses relative to sea level thus

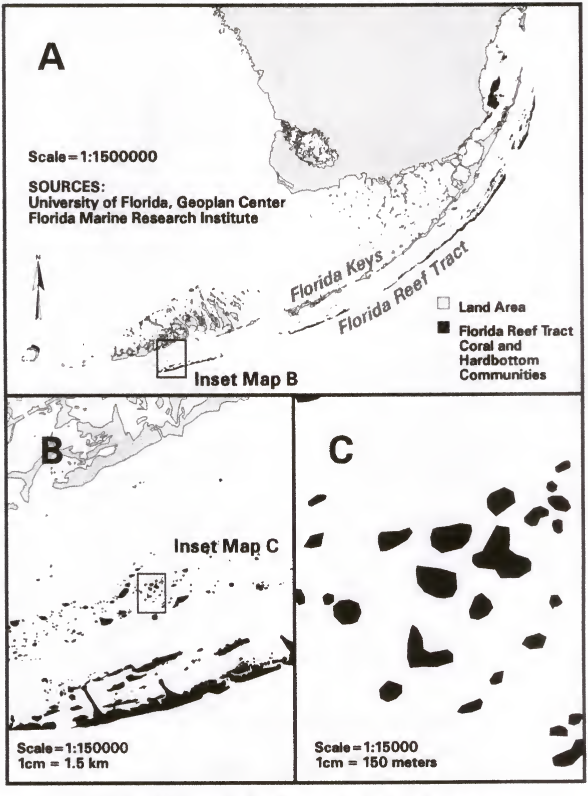

Figure 1.2. Reef Morphology in the Florida Reef Tract. The Effects of Scale Across 3 Orders of Magnitude. A) Macroscale Morphology (1:1,500,000-Scale). B and C) Mesoscale Morphology (1:150000-Scale and 1:15000-Scale).

affecting the placement of marine substrata in relation to the photic zone. Both affect the placement and movement of ocean currents that determine the spatial distribution of warm tropical waters and may carry nutrients, pathogens and marine larvae. Climatic variations may raise or lower sea levels both increasing and eliminating suitable substrata for coral growth. Such processes operate over periods of thousands to millions of years. They may have periodic or discontinuous frequencies that are not well understood but which have left spatial footprints on the landscape.

Temperature and currents

Incoming solar radiation (insolation) differentially heats the oceans creating great gyres that redistribute heat from the equator towards the poles. These are blocked and directed by the placement of continents, extending the influences of warm oceanic waters poleward along the east coasts of landmasses and contracting them equatorward along western coastlines. Guilcher (1988) states that the spatial pattern of coral reefs can be primarily explained by the distribution of sea surface temperatures in the 17 to 34 °C range, which reflects the limits of normal coral growth. Low temperatures associated with upwelling currents along the western coasts of otherwise tropical landmasses are widely cited as the reason for the absence of coral reefs from these areas. Thus, coral reefs are concentrated within about 15 degrees of the equator, showing poleward extensions along the east coasts of continents that are associated with these 'tongues' of warmer waters and equatorward contractions along western continental margins.

The great oceanic currents associated with these heat-driven gyres may play an important role in providing nutrients to coral reefs in the otherwise nutrient-deficient (oligotrophic) environments of the tropical oceans. It is believed that much of the nitrogen and phosphorus supporting the high autotrophic production in these systems is obtained from dissolved and suspended organic matter that is strained from oceanic waters as they move across and through the reef (Sorokin, 1990b; Erez, 1990). Many studies have observed that coral growth tends to be most prolific and reef structures best developed on their seaward faces; those areas most exposed to the turbulence of currents and waves (Stoddart, 1969; Roberts, 1974; Hopley, 1982).

Geologic and climatic controls

Active coral growth is limited to hard, sediment-free substrata in the upper few meters, or photic zone, of the world's tropical oceans. Differential movement of these submarine surfaces relative to sea level is affected by geologic and climatic processes operating over relatively large areas and long time intervals. These are believed to provide the primary controls on small-scale reef development patterns within the temperature regimes that allow active coral growth. They also provide the foundation for general reef theory and reef classification (Hopley, 1982; Guilcher, 1988).

Charles Darwin is credited with being the first to recognize the linkage between geologic forces and macroscale reef morphology. He introduced the scheme for classifying coral reefs into three main types: fringing reefs growing close to a higher landmass, barrier reefs separated from the landmass by a lagoon, and atolls that consist of a reef enclosing a lagoon where there is no landmass (Guilcher, 1988). These were developed to explain his theory of subsidence in the origin of Pacific atolls. Here, a coral reef growing along the perimeter of a volcanic mountain stands at greater and greater distances from the shoreline as the island slowly subsides, ultimately leaving only a ring of coral.

Darwin's subsidence theory has survived to the present with qualifications arising from the accumulation of scientific evidence regarding climatic processes and events. His theory was developed prior to the general acceptance of continental glaciation with its attendant shift in sea levels during the Pleistocene (Stoddart, 1969). Thus, periodic marine transgressions and regressions in combination with tectonic forces such as subsidence have provided changing growth environments for coral-reef ecosystems. Stoddart (1969) notes that modern reef growth during the Holocene represents a relatively thin accretion on much older foundations, suggesting that the gross morphology and spatial distribution of present-day reef systems have developed over very long periods of time.

Mesoscale Morphology and Processes

At larger scales, reef structures begin to show discontinuities and a general rounding of the dominant linear theme. Here, antecedent topography, wave energy and biogeomorphic processes shape the component forms of the reef complex into elongated or patchy physiographic zones of active coral growth and sedimentary deposition. Here too, tropical storms and periodic outbreaks of disease and predators leave their marks on the landscape. At scales ranging from hundreds of meters to tens of kilometers, the generic composite of the reef system becomes distinct assemblages of smaller reefs, which develop around topographic forms within the smaller-scale reef structure. Hopley (1982) notes that smaller reefs form complex spatial patterns within the small-scale structure of the Great Barrier Reef of Australia, which are believed to be related to antecedent topography and wave-energy gradients.

Examples of scale-specific differences in mesoscale morphology are shown in Figures 1.2B and C for one area of the Florida Reef Tract.

Wave energy and geomorphic patterns

Hermatypic organisms grow in tropical waters wherever photic, substrate and turbidity conditions provide the proper environment. However, their structures and spatial assemblages are heavily influenced by wave energy and water turbulence. Coral growth tends to increase directly with wave-power conditions (Roberts, 1974; Roberts et al., 1975, 1977). In part, this is due to decreases in sedimentation and increases in the supply of nutrients and the removal of metabolic waste products associated with increasing water circulation (Stoddart, 1969; Roberts, 1974; Erez, 1990).

Areas of greatest coral growth are concentrated along the windward periphery of the reef from the reef crest to the forereef slope. In his study of Grand Cayman reefs, Roberts found that increasing wave energy conditions resulted in greater biomass per unit area and an increasing spatial density of structural elements such as spurs and buttresses (Figure 1.1). These constructional features function as effective breakwaters in a high-energy environment and maximize the surface area of the reef front (Roberts, 1974).

These same forces which serve as catalysts to growth as energy increases along the hydrodynamic curve begin to break, pulverize and redistribute pieces of the reef at higher energy levels. These erosional forces are typically associated with waves generated by various-sized tropical storms. They range from relatively small events that frequently break small pieces from the reef, to huge, cataclysmic cyclones that can pulverize a reef in a matter of hours (Stoddart, 1969, 1974).

The accumulation of such events over centuries and millennia modifies the general morphology of the reef into zones which grade from those of active growth, dominated by living hermatypes, to those which are exclusively environments of deposition, composed of detrital materials of various sizes and shapes. Such sediments tend to accumulate in the lee of the energy profile whereas corals concentrate along the higher-energy edges of reef platforms (Figure 1.1). Such facies grade to mutually exclusive environments where sediment is rapidly flushed from high-energy locations and is deposited in the lowest-energy locations (Stoddart, 1969; Hopley, 1982; Guilcher, 1988).

Physiographic zonation patterns

Coral reefs show distinct physiographic zonation patterns both laterally and transversely. Laterally, these zones are a result of exposure to wave energy. Transversely, they result from steep environmental gradients which grade from the reef front to the lagoon (Stoddart, 1969). Hopley (1982) classifies five general zones: the windward reef front; the outer reef crest; the inner reef flat; the lagoon, and; the leeward reef margins (Figure 1.1). These zones tend to develop in linear bands normal to the predominant wave direction and become less pronounced with declining wave energy. They grade from high-energy life zones dominated by active coral growth, massive constructional features and a low concentration of sediments, to low-energy depositional zones dominated by sediments and minimal coral growth.

The windward reef front and outer reef crest are the high-energy zones of the reef. Their outer surfaces are areas of prolific coral growth and minimal sedimentation. The best developed of these zones consists of steep, continuous, 'hard-line' reef fronts broken periodically by surge channels and extensive spur and groove formations. The leeward portion of the outer reef crest usually consists of an extremely smooth surface of packed coral rubble, or pavement, which may be cemented by crustose coraline algae. On many reefs, this feature may grade along its inner margins into moderately or poorly sorted ridges of rubble or shingle that are composed of coarse materials broken from the reef front (Hopley, 1982; Guilcher, 1988). The inner reef flat and the lagoon are zones of decreasing relative energy, which form in the lee of the outer reef margins. Lagoons form extensive, well-developed features in certain platform reef systems, in oceanic atolls, and landward of many fringing reefs. Elsewhere, they may be small, pond-like structures on reef-top surfaces. The outer edges of the inner reef flat may support zones of dense or patchy coral growth in the decreasingly turbid areas immediately leeward of the reef crest. This zone grades into a lagoonal environment dominated by sediment deposition and minimal coral growth (Hopley, 1982; Guilcher, 1988).

The leeward margins of reef systems differ extensively depending on the underlying reef structure and wave energy exposure. Wave energy is generally lower along the leeward edge of any reef system. However, certain reef shapes will tend to focus more energy to the lee through refraction than others do. On more ovoid reefs, extensive patch reefs may develop with interlocking sand chutes that resemble a more open system of spurs and grooves. On ribbon reefs and many crescentic reefs, the leeward sand slope is almost continuous (Hopley, 1982; Guilcher, 1988).

Microscale Morphology and Processes

At very large scales, the morphology and topological complexity of coral-reef substrata reflect the spatial distribution and physical characteristics of their constituent biotic and abiotic elements. Across the smaller-scale physiographic zones, unique morphologic assemblages develop displaying a wide range of textural patterns. High-energy peripheral zones of active coral growth have textures that reflect the range of morphologies which corals and other hermatypic organisms can achieve across varying energy gradients. This is in contrast to low-energy, depositional zones where texture is imparted by the size and sorting of bioclastic sediments and benthic organisms such as sea grasses. Studies have identified a number of biologic and morphologic zones that develop across this constructional-depositional gradient.

Hermatypic organisms are segregated into distinct assemblages based on wave-energy regimes. Zonation studies conducted by Geister (1977) and Done (1983) indicate that coral growth forms show distinct zonation patterns that are more attributable to energy gradients than to species assemblages. Hopley (1982) notes that the Scleractinia are highly plastic organisms whose species-specific colonial shapes may cover a wide range of forms under varying environmental conditions. The highest energy zones are typically dominated by calcifying algae and encrusting or ridge-shaped corals whose structure can resist tremendous wave action (Figure 1.1). As wave energy is attenuated, large, wave-resistant corals begin to dominate. At greater depths, these are replaced by more delicate forms (Achituv and Dubinsky, 1990).

Geister (1977) identified six ecological reef zones in the Caribbean that could be classified by their distinct assemblages of coral species and their decreasing exposure to wave action. The zones were roughly parallel to each other and were located at various depths depending on the wave energy in that location. Certain zones disappeared entirely in areas where sea-bottom topography and/or energy levels were not conducive to their formation. Geister's study indicates that coral assemblages having the greatest vertical relief and living surface intricacy are developed in intermediate energy zones. Here, dense thickets of branching Acropora (palmata and cervicornis) with mixtures of glomerate brain corals (Diploria strigosa) create very rugged landscapes. At higher and lower wave-energy levels, surface relief becomes much less pronounced as morphologies grade to either encrusting algal ridges or sand and rubble flats with dispersed glomerate coral heads (Geister, 1977).

Geometric Properties of Coral-Reef Substrata

At very large scales, the geometric textures of coral-reef substrata are dependent on the density and growth forms of the resident benthic organisms, the size and sorting of existing bioclastic materials, and the characteristics of interstitial spaces or cavities in the biogenic surfaces. Surface area is dependent on the three-dimensional characteristics of the substrata and the scale at which the measurements are made. The literature suggests that this geometry is extremely complex and covers scales ranging from at least microns to meters. Dahl (1973) states that surface area is a very important parameter in coral-reef ecology. Control of surface and interstitial spaces by secondary occupants is "a basic competitive force and a major determinant of reef communities (page 240)".

Many qualitative observations of these textural patterns have been made, but the literature yields very few quantitative studies. Ginsburg (1983) notes the highly complex, variably sized network of cavities that comprise living reef systems. Spaces in living coral zones may range from the relatively ordered intraskeletal cavities between cells and coral polyps (20-500 μm) to the highly irregular cavities between coral branches, plates and colonies (1-100 cm). These spaces are compared to interparticle cavities in sediment which may range in size from tens of microns for silt and fine sand particles to centimeters within coral rubble (Ginsburg, 1983). Even greater spacing occurs between larger-sized substrate elements such as spurs and small patch reefs. The organic and biogenic elements that form the substrata should show a similar size progression since they produce the observed cavity structure.

Such observations suggest that the size and spacing of geometric substrate elements together with their surface area increase from sand-dominated to coral-dominated areas. Luckhurst and Luckhurst (1978a) provided quantitative measures indicating that the three-dimensional surface area, or rugosity, of coral substrata are many times those of sand environments and that measures of substrate relief were highly correlated with rugosity. Dahl (1973) made surface-area measurements across a section of the Belize Barrier Reef as a ratio of distance along the substrate surface to straight-line distance. This 'surface index' ranged from 1.0 for featureless sand substrata to 15 for the highly complex reef crest. Between these extremes were sea grass, fine rubble, coarse rubble and patchreef substrata with surface indexes of 3.5, 1.08, 2.5 and 5 respectively. The reef crest and patchreef surface indexes were estimates constructed for a theoretical reef surface composed of different surface types or geometric elements at three unique scales. These corresponded to gross reef morphology with its associated ridges or spurs and grooves, individual coral colonies shaped as hemispheres, plate-like ridges or branched cylinders and very small, conical, coral-polyp cups occurring on colony surfaces. Scale-specific, reef-crest surface indexes were calculated at 1.57, 2.75 and 3.55 respectively (Dahl, 1973). Multiplication yielded the composite index of 15.27.

Only a few studies have analyzed the continuity of size progressions in the structural elements comprising the coral-reef environment. Stoddart (1979) notes that discrete size clusters may occur in reef sediment distributions because of the morphological organization of the parent material. Acropora colonies, for example, have been shown to yield two discontinuous size modes upon disintegration: sticks associated with the fragmentation of the colony, and grit associated with the constituent cells of the coral polyps (Folk, 1962, as cited in Stoddart, 1979). Bradbury et al. (1984) found three discontinuous clusters of organizational elements with different fractal dimensions across a reef front in the Great Barrier Reef of Australia. They noted that the branches and convolutions of individual coral colonies clustered in the 10-cm range while living adult coral colonies ranged in size from 20 to 200 cm. Larger geomorphologic features such as spurs, grooves and buttresses clustered in the 3 to 5-m range. Between these clusters they observed sharp breaks in the values of their fractal index which they interpreted as indicating 'real changes in the processes causing patterns in the reef surface' (Bradbury et al., 1984).

Hierarchy Theory and Ecosystem Organization

Simon (1973) and O'Neill et al. (1986) note that all biological organizations are composed of 'intertwined sequences' of relatively stable sub-assemblages which are bound together into larger functioning units across a wide range of temporal and spatial scales. This hierarchical structuring of natural systems confers geometric textures on landscapes, which result from the size and spacing of individual components and their vertical and horizontal organization into smaller-scale assemblages. On coral reefs, autotrophic zooxanthellae are clustered within coral polyps, which are organized into colonies that are organized into reefs. At each organizational level, the outputs of multiple sub-assemblages or components come together across two or more spatio-temporal scales into relatively stable, higher-level organizations. Organizational elements and their spacing become larger across scales and may show both vertical and horizontal discontinuities as processes change.

Vertical Organization in Hierarchies

Organization within the hierarchy is visualized as resulting from significant 'differences in process rates' which occur at increasing levels of organization along the space-time continuum (O'Neill et al., 1986). The lowest levels of any hierarchy are dominated by fast, high frequency processes that become progressively slower and of lower frequency at higher levels due to integration of the outputs of many lower-level components. Thus, the higher-level organization responds more slowly over increasing temporal and spatial scales to longer-term changes in the averages of these outputs. This characteristic, referred to as 'loose vertical coupling,' may effectively isolate each level from the other, insulating the higher-level organization from perturbations affecting some of the lower-level components (O'Neill et al., 1986). Simon (1973) notes that the higher-frequency dynamic behavior of the lower-level components is irrelevant to higher levels in the hierarchy. Only the equilibrium properties affect the smaller-scale (higher-level) assemblage.

On coral reefs, such vertical structure can be seen in the symbiotic association between thousands of photosynthetic, unicellular algae which provide reduced organic carbon and oxygen to a single coral polyp (Hopley, 1982). Whereas the algae respond very rapidly to changes in light intensity in combination with metabolic by-products received from the host, the polyp responds to the average of these inputs in combination with other internal and external components. At higher levels of reef organization, small colonies may contain thousands of polyps and small reefs thousands of colonies. In this example, each level is separated in size by at least three orders of magnitude. The fast, short-lived alga cells may complete their life cycle in a matter of days or weeks whereas the life span (replacement time) of a small reef may be a thousand years or more. Each higher level exists because of its constituent components, but its spatial and temporal dynamics and geometry are those of their equilibrium properties.

Horizontal Organization in Hierarchies

Organization, as defined by process rates, also occurs horizontally in hierarchies. Since interaction declines with distance, spatial discontinuities in process rates occur within levels. Thus, organizational components interact more frequently or at faster rates within the bounds of the higher-level organization or 'holon' than between. Such characteristics, referred to as 'loose horizontal coupling', result in discontinuous spatial concentrations or clustering of components into subsystems (holons) at various scales (O'Neill et al., 1986). The dynamics of the algal assemblage are those of the interaction of its internal components operating in combination with its surrounding environment within the bounds of its cellular membrane. Interaction rates between algae are slower and become the dynamics of the next level in the hierarchy.

At decreasing scales on the reef, the symbiotic algae are spatially concentrated in the flesh of coral polyps, which are concentrated into higher-level assemblages of colonies and reefs. At each new level, tangible or intangible boundaries may be defined by changes in rates or thresholds where the relatively rapid interaction of components within each holon give way to lower rates between holons (O'Neill et al., 1986). Thus, the photosynthetic process that is a critical input to each higher level of organization on the reef is discontinuously clustered into nested sets of assemblages within the bounds of each higher level in the hierarchy. At each new level, there is an abrupt transition in size and distance between the nested sets of lower-level components that reflect the dynamics of the new organizational level (Holling, 1992). These clusters and gaps define the texture or grain of the assemblage at each level in the hierarchy. Holling (1992, 1995) suggests that such clusters become the dominant frequencies of the landscape around which other processes and components are entrained.

Changes in process rates, which occur across environmental gradients, affect the spatial characteristics of organizational sub-assemblages within the reef surface. High-energy, coral-dominated peripheral zones may change abruptly to low-energy, leeward zones of bioclastic deposition. These, in turn, may be subdivided at larger scales into morphologic zones whose textural characteristics reflect wave-energy gradients and the size, forms and spacing of benthic organisms or bioclastic sediment.

The Morphology of Animals and Landscapes

Various authors have suggested that the physical architecture of the environment may shape the morphology and community structure of animals that occupy particular landscapes (MacArthur, 1958, 1972; Holling, 1992, 1995). In his studies of birds and mammals of the boreal forest and short-grass prairie, Holling (1992) noted 'clumpy' distributions in adult body sizes that could not be explained by random processes, taxonomy or trophic characteristics. Instead, they appeared to be correlated with the 'coarseness of grain or texture of the habitats' chosen by species within each 'clump' for their foraging bouts. Animals of similar size chose similar-sized landscape elements in which to feed. Based on these observations, Holling (1992) proposed a 'Textural-Discontinuity Hypothesis' which states that animals occupying a landscape should have body sizes which cluster around textural frequencies which are associated with that landscape. As such, these body size clusters represent a bioassay of hierarchical structures within landscapes.

Hierarchy theory suggests that there are many more small elements contained within a landscape than large ones. If animals measure the spatial grain of resources (food and shelter) in their environment as a function of their size, then small animals will exploit small-grained resources and have smaller home ranges since there is a greater density of resources per unit area. Larger animals will exploit larger-grained resources that have a lower unit-area density. Larger home ranges offset this difference (Holling, 1992, 1995). If animal sizes show such relationships, then the number of animals by size category should show a general decline across scales. This would be consistent with the general ecological concept of biomass pyramids. Odum and Odum (1955) noted such a structural arrangement in the trophic organization of the reef at Eniwetok Atoll. Across fractal surfaces, this relationship should display a power function reflecting a continuous (self-similar) hierarchical organization across scales. Morse et al. (1985) found just such an inverse power function when relating arthropod body lengths to the number of individuals collected from vegetation surfaces in several areas of the world.

If the geometry or textures of landscapes are spatially distributed in discontinuous textural assemblages, then the resources utilized by animals will likely be as well. Thus, resources will exist in discrete clusters separated by breaks at different scales. Gaps should occur in the size distributions of animals at those points where there are grain-specific breaks in the spatial architecture of landscapes (Holling, 1992). In other words, these gaps will exclude certain animal sizes. Schwinghamer (1981, 1985) demonstrated that benthic organisms in near-shore, abyssal and continental shelf communities have distinct body-mass clusters that are correlated with the textures of the sediments they occupy. Bacteria and related organisms were associated with the surface texture of silt particles. Intermediate-sized biota lived in the interstitial pores between particles, while the largest organisms were associated with the texture of the substrate as a whole.

Within landscapes, the size and magnitude of animal body-mass concentrations may depend upon the extent to which particular scale-specific textural frequencies are developed in the landscape architecture. Holling (1992) observed that very similar body-mass clusters persisted across ecosystems. Some disappeared. Others appeared or were sub-divided. Their magnitude (as defined by the number of species present) changed, but their boundaries, while not identical, were 'strikingly similar' (Holling, 1992). This he attributed to certain universal textural characteristics, which result from similar ecological and landscape processes operating across different ecosystems. The range and intensity of textural scales present in any one landscape or ecosystem change, thus changing the magnitude of animal body-mass clusters associated with these frequencies. Certain body-mass clusters may disappear in ecosystems where particular textural frequencies are reduced or eliminated. Holling observed that boreal forest bird 'clumps' associated with the fine-grained, three-dimensional canopy of the forest were reduced or eliminated in the short-grass prairie. Similarly, a new size clump of species emerged in the prairies which was associated with its geometrically dispersed pattern of isolated trees and shrubs (Holling, 1992).

Since different marine environments have unique geomorphologic properties that result from different operational sets of biotic and abiotic structuring processes, it stands to reason that they may have unique sets of structural textures. If the Textural-Discontinuity Hypothesis is correct, then they should also have very different assemblages of resident organisms in terms of size and body-mass concentrations.

Coral-Reef Fish Communities

Tropical fish are an integral part of the biota of any coral-reef community. Aside from the structuring benthic organisms, they are perhaps the most visible and extensively studied populations on the reef. Their abundance and diversity are well documented. Coral reefs are believed to produce more fish than any other natural system on the planet (Saila et al., 1993). Nearly 2,000 species are known from the northern end of the Great Barrier Reef alone (Sale, 1978). As major secondary producers, they range the trophic spectrum from herbivores, to carnivores, to scavengers. Sutton (1983) noted similar trophic distributions from reefs in many tropical areas. While reefs provide food and shelter, little is known about their community structure, dynamics and microhabitat requirements (Bohnsack et al., 1985). Quantitative studies have been conducted mostly on small reef sections, or areas involving isolated patch reefs, individual coral heads, or artificial reefs (Bohnsack et al., 1985; Sale, 1991).

Community Structure of Coral-Reef Fishes

Reef fish community structure has been visualized as a combination of stochastic and deterministic processes. Regional fish populations supply the pool of gametes/larvae, which are the source of recruitment for replenishing individual patches of reef habitat (Sale, 1978, 1991; Smith, 1978). Stochastic prerecruitment factors such as ocean currents, weather, larval mortality and the availability of unoccupied habitat are believed to account for the high spatial and temporal variations in abundance and diversity that are observed within and between small sites (Sale, 1978, 1991). Smith (1978) describes these processes as a series of screens or random barriers to colonization which include predation. Random patterns also result from the fact that small habitat patches can only accommodate a portion of the species in the regional faunal pool (Sale, 1991).

Community structure may also be influenced by deterministic processes associated with morphologic and behavioral adaptations and competition. Certain adaptations in morphology such as the mouth structures of herbivores determine what resources are exploited on the reef. Behavioral adaptations such as diurnal and nocturnal feeding habits temporally partition the use of resources. Such resource-sharing mechanisms permit specific species to take advantage of different resources within the reef ecosystem (Helfman, 1978; Smith, 1978). Interspecific competition is considered by some to be a major factor in community structure (Smith and Tyler, 1972; Smith, 1978). Others such as Sale (1978, 1991) believe that random factors may be of equal or greater importance.

Various authors suggest that space may impose greater limitations on reef organisms than predators or food. Smith (1978) notes that reefs appear crowded, with every surface and opening utilized by some organism. Sale (1978) concluded that all available space in his study of territorial pomacentrids was usually occupied, and when vacated, quickly reoccupied. Artificial reef studies have found similarly rapid colonization (Hixon and Beets, 1989; Bohnsack et al., 1994). Since space is related to the size of the reef patch, community characteristics may vary between patches. Bohnsack et al. (1994) found that larger reefs had larger fish and greater biomass, whereas smaller reefs had greater abundance per unit area and smaller fish. Species diversity was found to be greater on multiple small reefs than one larger reef of similar mass (Bohnsack et al., 1994).

Habitat Structure and Coral-Reef Fish Communities

Just as coral-reef benthic communities show spatial patterns in primary production, physical structure and species assemblages, so too do coral-reef fish populations. Many authors have noted the concentrations of fish that occur in association with coral reefs (Bohnsack et al., 1985; Saila et al., 1993). At these scales, fish populations may develop large standing crops (Goldman and Talbot, 1976; Mensaveta et al., 1986; Montgomery, 1990) which reflect the primary productivity of the reef in comparison to the surrounding ocean. At larger scales, fish abundance and composition has been shown to differ between physiographic reef zones. Sale (1991) notes that numerous authors have documented that different zones have consistently different fish-species assemblages that are persistent across geographic regions. Harmelin-Vivien (1977) concluded that fish abundance, diversity and species assemblages changed dramatically across vertical zones on the outer slope of Tulear Reef, Madagascar. Such studies suggest that fish abundance and community structure may be related to biophysical differences between reef zones that affect the spatial distribution of shelter and trophic web characteristics.

Many authors have noted an apparent relationship between fishes and habitat structure, particularly as they affect shelter characteristics (Bardach, 1959; Randall, 1963; Talbot, 1965; Jones and Chase, 1975; Goldman and Talbot, 1976; Gladfelter and Gladfelter, 1978; Shulman, 1984). Hixon and Beets (1989) note the existence of a 'long-standing Limited Shelter Hypothesis' which suggests that appropriately-sized structural shelter may limit reef fish populations. The availability of shelter spaces of particular sizes presumably limits the total number and size structure of fish populations through its effects on predation rates (Shulman, 1984). Artificial-reef studies have shown that the availability of small shelter spaces dramatically improves the survival rates of juvenile reef fishes (Shulman, 1984; Gorham and Alevizon, 1989). Hixon and Beets (1989) noted a significant negative relationship between the number of resident piscivores and the number of small prey fishes on their artificial reefs.

A number of studies have compared fish abundance, species diversity and biomass with various measures of habitat complexity. Species richness or diversity has been found by some authors to be correlated with substrate habitat complexity (Talbot, 1965; Talbot and Goldman, 1972; Risk, 1972; Luckhurst and Luckhurst, 1978a; Molles, 1978; Talbot et al., 1978; Shulman, 1984). Structural habitat complexity has been positively correlated with fish abundance in some studies (Luckhurst and Luckhurst, 1978a; Shulman, 1984) but not in others (Risk, 1972; Sale and Douglas, 1984). Roberts and Ormond (1987) found that the number of substrate spaces in three size groupings accounted for 77 percent of the variance in fish abundance at some Red Sea sample sites. Bell and Galzin (1984) concluded that percentage live coral cover was significantly correlated with the total number of fish species and individuals in lagoonal areas at Mataiva Atoll. Some authors have found more species, individuals and body mass associated with complex branching coral forms (Hiatt and Strasburg, 1960) or more rugged structural complexes such as the spur and groove zone (Harmelin-Vivien, 1977).

While spatial heterogeneity is thought to be an important structuring element in determining the abundance, distribution and diversity of coral-reef fish (Shulman, 1984), few studies have attempted to link their size and body-mass concentrations to specific geometric properties of various coral-reef substrata. Luckhurst and Luckhurst (1978a) constructed 'substrate rugosity' indexes for various reef transects in Curacao and Bonaire. These linear measures of 'gross reef morphology' (surface area to straight-line distance) were found to have significant positive correlations with the number of fish species greater than 5 cm in size. Other authors have noted positive correlations between substrate hole size and fish body size (Randall, 1963; Robertson and Sheldon, 1979). Smith (1978) suggests that such observations indicate 'a genetic or adaptive relationship' between reef habitat cavities or openings and fish sizes, which he notes, are 'notoriously plastic'. In an experiment using artificial reefs, Hixon and Beets (1989) found a direct relationship between the size of fishes recruiting to their reefs and the artificially-constructed hole sizes. They note, however, that similar studies have not been attempted on large coral reefs.

CHAPTER 2
POSING THE QUESTIONS

The primary purpose of this work is to test the proposition that the structural characteristics of coral-reef fish populations, specifically their size, mass and abundance, are organized into specific patterns that reflect the physical geometry and hierarchical organization of coral-reef ecosystems. This research will test two parallel and interrelated hypotheses which suggest that reef fish populations are characterized by discontinuous clusters of sizes, mass and behavioral adaptations which are directly related to similar geometric reef properties that are generated by a small set of processes that structure coral-reef environments. Biogeomorphologic textural frequencies are generated by the hierarchical organization of hermatypic organisms and their assemblages, which are themselves, constrained and spatially organized by wave-energy gradients. Morphological clusters of fishes develop around the dominant frequencies of reef-system environments, which provide food and shelter across a limited range of scales. In this sense, fish body sizes become a bioassay of reef ecosystem structure (Holling, 1992). This effort represents the continuation of a limited study conducted in 1994 which found that discontinuous clustering of body sizes did occur in coral-reef fish populations at Looe Key National Marine Sanctuary in Florida (Breedlove and Donahue, 1994).

This proposal borrows heavily from two existing sets of hypotheses. The first suggests that the spatial architecture of biotic communities and landscapes are structured by certain keystone variables and processes into discontinuous assemblages. This argument was made by Paine (1966, 1974) in his study of spatial patterns in littoral mussel communities resulting from starfish predation. This 'Keystone Hypothesis' was expanded by Holling (1992) by suggesting that all terrestrial ecosystems are hierarchically structured by a small number 'of key plant, animal and abiotic processes' that focus ecosystem organization into discontinuous clusters, each of which has its own limited range of scales. The second set of hypotheses suggests that the morphology of resident animals in particular ecosystems may be related to the geometric structure of the landscapes they occupy. Holling (1992) proposed a Textural-Discontinuity Hypothesis which states that the hierarchical organization of landscapes should be demonstrated by discontinuous distributions of 'animal sizes, searching scales, and behavioral choices'. The dominant frequencies of such 'bioassays' should change across landscapes having different hierarchical structures (Holling, 1992). An important corollary to this proposition, the Limited Shelter Hypothesis, has been proposed by a number of ecologists in various forms (Smith and Tyler, 1972, 1973; Sale, 1978, 1991; Smith, 1978). It states that appropriately-sized structural shelter is a 'primary limiting resource for reef fishes' (Hixon and Beets, 1989).

While it is known that the physical structure and biotic composition of coral-reef ecosystems change across space, their organizational properties are poorly understood. Very little data exist to indicate whether the biotic and abiotic components of coral-reef ecosystems are organized into unique, discontinuous clusters of relationships or textural assemblages whose frequencies reflect sets of 'keystone' structuring processes as suggested by Holling (1992) and predicted by hierarchy theory (Simon, 1973; O'Neil et al., 1986). Bradbury et al. (1984) suggest that such organizational patterns do exist on at least three separate scales on one reef crest of the Great Barrier Reef of Australia. Animal size clusters have been identified and correlated to the geometric properties of sediment and their interstitial cavities in near-shore and abyssal marine communities (Schwinghamer, 1981, 1985). Coral-reef fish populations have been shown to display discontinuous body-size clusters on one Florida reef (Breedlove and Donahue, 1994). Fish species greater than 5 cm in length have been positively correlated with measures of gross reef morphology (Luckhurst and Luckhurst, 1978a) and at least one artificial reef study has shown that fish size composition is directly related to the size of shelter cavities (Hixon and Beets, 1989). However, no known study has attempted to examine such relationships across physiographic environments within a large coral reef system.

Formulating the Hypotheses

Geomorphologic studies suggest that great structural variations exist between physiographic reef zones which are attributable to the morphology of the structuring organisms and the geophysical processes which shape their environment. Topological complexity, or reef structure, has been found to be directly related to wave energy (Roberts, 1974; Bradbury and Young, 1981) as has coral morphology (Done, 1983) and, to a lesser extent, coral community structure (Bradbury and Young, 1981). At larger scales, the geometric patterns of reef substrata are related to the morphology of the structuring benthic organisms, both living and dead, and the range of forms they assume in response to energy flows within the coral-reef environment. Zones dominated by living corals are much more rugged than those that are primarily depositional environments. Ginsburg (1983) noted the highly complex, variably-sized network of cavities that comprise living reef systems, while Dahl (1973) and Luckhurst and Luckhurst (1978a) provided quantitative measures indicating that the three-dimensional surface area of coral substrata are many times those of rubble and sand flat environments. Zonation studies conducted by Geister (1977) and Done (1983) indicate that coral growth forms and their assemblages are highly plastic, adapting their geometric properties to the energy gradient.

Such observations strongly suggest that coral reefs are spatially organized by hierarchical processes into physiographic zones with specific ranges of geometric properties (object sizes and interobject distances) that change dramatically across environments within the reef system. Landscape textures range from fine-grained, low-relief sandflat environments to complex, high-relief three-dimensional coral assemblages. At large scales, hermatypic organisms and wave-energy gradients are believed to be the 'keystone' processes, which shape these zones and the range of geometric textures that occur in intrareef landscapes. Are reef elements and their interstitial spaces/cavities organized into hierarchies that cluster around particular frequencies associated with the structuring processes? Do these frequencies and their ranges change across reef environments? These questions are related to the Keystone Hypothesis of Paine (1966, 1974) and the Extended Keystone Hypothesis of Holling (1992). They can be restated in the form of a testable hypothesis.

> Coral reefs are hierarchically organized by a small set of 'keystone' processes into discontinuous biotic and abiotic assemblages across scales. Each hierarchical assemblage has a specific range of object sizes and interobject distances (geometric properties or textures) which change abruptly at organizational boundaries where processes change.
>
> Null Hypothesis: There are no significant discontinuities or clusters in the organization of coral-reef ecosystems. Geometric properties show random and/or continuous gradations between environments.

The literature suggests that biologic productivity in coral-reef ecosystems is spatially concentrated into linear and patchy zones which reflect patterns of wave energy and light intensity on the reef (Larkum, 1983). The highly productive forereef margins act as organic source zones whose excess primary production is carried down the energy gradient to be deposited on sand flats or in lagoons which act as organic sinks (Kinsey, 1983). Primary production itself is largely associated with either free-living or symbiotic algae which take on many forms ranging from encrustations of coraline algae, to low-lying mats and patches of benthic and turf algae, to three-dimensional clusters of zooxanthellae contained within the structuring corals (Hopley, 1982; Larkum, 1983; Sorokin, 1990a). The spatial concentration and distribution of these autotrophs must play an important role in structuring the organic and geometric properties of food and shelter on the reef.

If the general trophic structure within coral-reef ecosystems has the pyramid shape predicted by ecological theory (Odum and Odum, 1955), then secondary production within the ecosystem should show spatial variations that are related to those of primary production which forms the basis of the food chain. Heterotrophic abundance should display a similar distribution when ranked by size, reflecting the hierarchical organization of landscape elements into larger and less numerous assemblages (Morse et al., 1985; O'Neill et al., 1986; Holling, 1992, 1995). If animals measure the spatial grain of resources (food and shelter) as a function of their size (Holling, 1992), then fish, which feed either directly on the primary producers (herbivores, planktivores and corallivores) or on other secondary producers (micro-invertivores, macro-invertivores and piscivores) should display size, mass and numerical characteristics which are a function of the resources they exploit. Total abundance should be indicative of patterns in primary productivity and specific food sources within the reef, while size distributions should reflect the hierarchical organization of the food chain and geometric patterns of food and shelter on the reef. The highly productive forereef margins and patch reef clusters should have higher concentrations of fishes per unit area than the low-energy sand flats and lagoons. They should also have larger fishes whose size concentrations reflect fundamental differences in the size of elements and spaces between environments. Such relationships should reflect structural changes in productivity and morphology that occur both horizontally and vertically within the reef system.

Fishes inhabiting coral reefs display differences in community characteristics that have been attributed to the physiographic and trophic characteristics of their environment. Both abundance and diversity have been associated with the presence of reef habitat. Trophic composition is expected to change as a function of food sources available in different environments. The general morphology of habitats has been associated with the size and life stage of fishes. Big reefs have been observed to have larger fish than small reefs (Bohnsack et al., 1994), and juvenile fishes are noted to congregate in shallower habitats (Helfman, 1978). Do coral-reef fish populations exhibit discontinuous size distributions or clusters of body mass, and are their morphologic characteristics related to the hierarchical organization of reef ecosystems? These questions are related to the Textural-Discontinuity Hypothesis proposed by Holling (1992) for terrestrial ecosystems and the Limited Shelter Hypothesis as stated by Hixon and Beets (1989). The following hypothesis is proposed for coral-reef ecosystems:

> Fishes occupying coral-reef landscapes should have body sizes that cluster around textural frequencies that are associated with these landscapes. Hierarchical structuring of the landscape should be reflected in the discontinuous distributions of fish body sizes and their behavioral adaptations such as foraging scales or home ranges. Reef environments having different hierarchical structures should contain

> fish populations having correspondingly different size and mass characteristics.
>
> Null Hypothesis: There is no significant relationship between the sizes of fishes inhabiting coral reefs and the texture of the landscapes they occupy.

Competing Hypotheses

Several additional hypotheses which might explain discontinuous distributions in fish body sizes and mass were also identified. Such alternatives arise from long-standing arguments in the body of ecological literature concerning the community structure of coral-reef fish populations. Random recruitment processes, interspecific competition and trophic characteristics have all been suggested as major community structuring factors. Each of these alternatives will be tested and evaluated in the course of this research. These competing hypotheses may be stated as follows:

> **The Stochastic Hypothesis.** Body-size clusters result from random waves of recruits settling into limited habitat spaces as they become available. Small habitats can sustain only a small fraction of the regional faunal community. Hence, body-mass and size-structure differences result from a random mixture of life-stage body sizes and species composition.
>
> **The Dominant Species Hypothesis.** Reef environments are dominated by a small number of successful species whose body-mass characteristics set the size frequencies observed in reefscapes. Thus, body-mass clusters reflect the structure of the dominant species, not the substrata.
>
> **The Trophic Hypothesis.** Fish body sizes are related to the size ranges of the physical elements of their diet. Planktivores, herbivores, invertivores and piscivores will dominate different size ranges, thus producing 'standing waves' or clusters in the body-size spectrum (Holling, 1992)

CHAPTER 3
STUDY AREA AND METHODOLOGY

If the morphology of fishes is to be systematically compared to the biogeomorphic structure of an entire reef system, then it is apparent that a very large, comprehensive database is required. Since reef systems contain numerous biophysical zones with dramatic structural variations, the site-specific sample size must be large enough to provide statistical significance for tests both within and between zones. The database must provide species-specific measures of fish size and abundance as well as measures of substrate characteristics. In this sense, the availability of the database has determined the study area chosen. The scope of this research was possible only because of the size of the reef-fish data base that has been collected and was most generously provide for the Florida Reef Tract by Dr. James Bohnsack and his colleagues at the National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory.

The Study Area and Data Sources

The Florida Reef Tract is an elongated system of living coral reefs and associated habitats that parallel the Florida Keys on their eastern, Atlantic Ocean margins (Figure 3.1). It extends for a distance of nearly 360 km from just south of Miami to the Dry Tortugas. While some have referred to it as a barrier reef, the current terminology refers to the reef tract as a 'bank reef system' (Smith, 1948; Japp, 1984). The macroscale reef structure occupies the outer

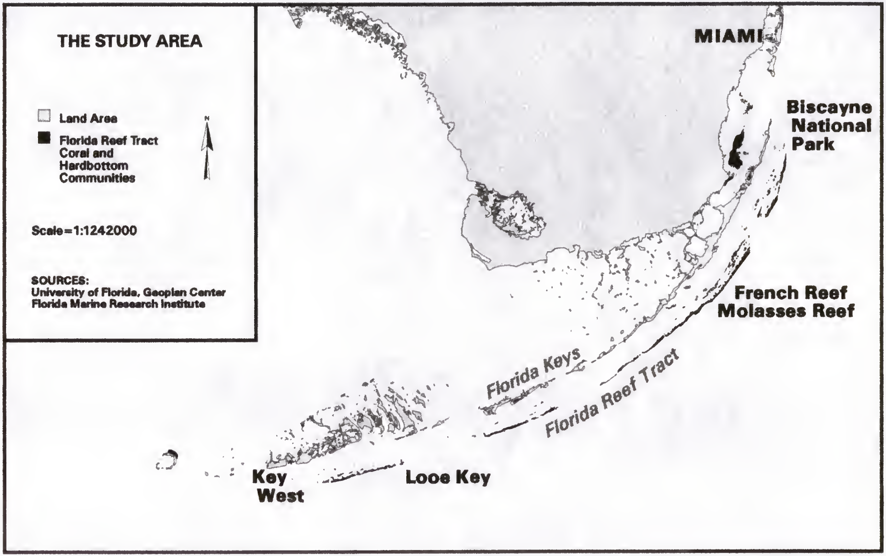

Figure 3.1. The Study Area.

portion of a narrow shelf which separates the emergent Keys from the deep waters of the Straits of Florida (NOAA, 1995). The main reef complex is separated from the Keys by the Hawk Channel. Within this bank reef system are contained a full range of physiographic reef zones and an extensive fish fauna. The high-energy outer edges of the main reef complex are characterized by linear discontinuities and standard forereef structural zones such as seaward-facing spurs and grooves (NOAA, 1995). Approximately 6,000 patch reefs are linearly distributed shoreward of the outer reef complex (Bohnsack et al., 1992; NOAA, 1995). Intermixed with these structural complexes are rock, rubble, sand and sea grass environments. Hardbottom structures associated with exposed Holocene calcium carbonate substrata also occur in the backreef zones.

Coral-Reef Fish Data

Fish data used in this study were collected by Dr. James Bohnsack and his colleagues at the National Marine Fisheries Service from selected sample sites within Biscayne National Park and the Florida Reef Tract over a period of 15 years. This database is one of the largest of its kind in the world. They were provided to me by Dr. Bohnsack at the request of Dr. C.S. Holling. The database includes species-specific measurements of fish length and abundance for 3,693 sample sites within the study area. Each sample is classified by habitat zone and proportion bottom cover by type. Maximum vertical substrate relief is included for 649 of the sample sites. A total of 72,334 individual species observations are contained in the database.

Data were collected using a stationary sampling technique described by Bohnsack and Bannerot (1986). This technique involves censusing all species and individuals observed by a diver within an imaginary cylinder of 24-foot radius extending from the surface to the bottom.

This procedure is divided into two phases. First, the diver would identify all species observed within the cylinder during a 5-minute listing period. Species likely to transit the cylinder were enumerated as identified. During the second phase, identified species were enumerated one at a time as the diver rotated 360 degrees (Bohnsack et al., 1992). Maximum, minimum and mean estimated fork lengths were recorded for each identified species to the nearest 1 cm.

Geographically, the 3,693 samples include sites from reefs and habitat zones across many areas of the Florida Reef Tract. Samples are included from 65 individual reef areas. Looe Key National Marine Sanctuary, Molasses Reef, French Reef, and Biscayne Bay National Park account for two-thirds of the sample sites (Figure 3.1). Fifteen habitat zones and nineteen bottom cover types are included in the site classification system (Table 3.1).

A number of limitations are noted for the fish sample data. Bohnsack et al. (1985) state that the samples should not be used for absolute density calculations since stationary samples probably underestimate true abundance. However, relative abundance should be quantitatively comparable between habitats and reefs (Bohnsack et al., 1985). Sites were sampled only during daylight hours, so certain nocturnal species may not be included. Similarly, certain species may be recorded in their foraging habitats away from the reef. Juvenile and adult life stages cannot be distinguished in the database. Finally, the species-specific counts and length measurements are, in many cases, estimates. Minimum, maximum and mean values provide a reasonable measure of size variance at any given site, but the actual distribution of individuals is unknown.

Several additional variables that will affect the analysis have been accounted for in data preparation. Large seasonal fluctuations in abundance have been noted by Bohnsack et al. (1992) and can be accounted for by dates on the samples. Biomass conversion formulas have

Table 3.1. Bottom-type classes, habitat types and data base occurrences.

Bottom Type	Data Base Occurrences
Coral	2910
Wall	341
Platform	501
Branching Corals (Acropora palmata)	383
Branching Corals (Acropora cervicornis)	97
Sand	2193
Sand/Rubble	254
Other (Unknown)	378
Rubble - Small	656
Large Rubble	304
Large Coral Heads	158
Soft Corals (Gorgonians)	1857
Overhangs	101
Open Water	23
Fire Coral	445
Coarse Sand	1
Sea Grasses	293
Massive Corals (Diploria)	34
Rock	799

Habitat	Data Base Occurrences
Fore Reef	2058
Lagoon	68
Hard Bottom	347
Grass Flats	42
Sand Flats	63
Deep Reefs	51
Patch Reefs	844
Buttress Zone	38
Walls (Deep Drop)	0
Inside - Damaged	15
Outside - Damaged	9
Inshore - Control	6
Offshore - Control	11
Wellwood Shipwreck - (Damaged Sites)	76
Wellwood Shipwreck – (Undamaged Control Sites)	63

been added to the database from results published by Bohnsack and Harper (1988). Since such weight-length relationships are only available for 33 percent of the observed species, the remainder have been assigned formulas based on mean family or body-shape relationships observed for the published species. Species-specific trophic class codes have been added. Species were initially assigned to one of eleven trophic classes based on published data in Bohnsack et al. (1985, 1992, 1994). Where published data were not available, assignments were made based on family trophic status where these were consistent between species. Many of these classes are mixtures of the six primary trophic groups (browsers, planktivores, herbivores, micro and macro-invertivores and piscivores) reflecting the fact that many fishes are generalists. For analysis purposes, all species were re-assigned to one of the six primary groups based on the highest trophic level contained in the mixed class. Thus, species coded as macro-invertivores/piscivores were re-assigned as piscivores. These groups were further condensed by lumping all invertivores into one group.

Coral-Reef Substrate Data

Unfortunately, quantitative textural measurements of individual substrate types are not readily available. The literature contains few physical measurements that would allow a comprehensive analytical comparison of one bottom-cover type to another. The reason for this may be simply that such measurements are extremely difficult to make. This is particularly true at scales that are relevant to fish. The textural scales of elements and spaces that provide food and shelter for most infaunal reef species probably range from millimeters to centimeters, while home ranges cover areas of centimeters to meters (Luckhurst and Luckhurst, 1978b; Sale, 1978).

The NMFS reef-fish database includes observations on proportion bottom cover by type for each sample site. While these data contain no physical measurements of elements and spaces in reef environments, the 19 classes can be aggregated into a logical textural progression. At one extreme, sand substrata form the finest-grained environments, characterized by very small elements and spaces of little to no local relief. They provide very little shelter except to burrowing organisms. Larkum (1983) notes the low autotrophic productivity in such environments, which is limited to a thin, essentially two-dimensional layer by light penetration. At the opposite extreme are high-relief, forereef coral structures that are characterized by a very large range of small to large elements and spaces. Autotrophic productivity is believed to reach a maximum in these environments due to extensive three-dimensional sunlit surfaces, the large concentrations of symbiotic zooanthellae and turf algae, and wave energy stimulus (Dahl, 1973; Done, 1983; Larkum, 1983). Between these extremes are rubble, rock and sea-grass environments. Rubble consists of piles, ridges and sheets of broken coral in various stages of decomposition. It is the only substrate type whose codes include measures of its geometric properties (Table 3.1). Its textural composition ranges from big (basketball size and larger), to small, to mixtures of fine rubble and sand. It is often colonized by turf and filamentous algae. Rock or 'hardbottom' environments are developed on exposed Holocene carbonates and, in certain cases, represent recently dead reef structures. Such structures have ledges, solution features, fracture systems and the remnants of reef-structure elements and spaces. They also support diverse macroalgae communities (NOAA, 1995). Sea-grass beds form dense, low-relief biotic structures characterized by an extensive, interconnected maze of spaces between plants.

Approach and Methodology

Holling (1992) has suggested that animal body-mass distributions represent a bioassay of the geometric characteristics of landscapes. If this is the case, then fish populations occupying substrata having such essentially different geometric properties should themselves display significantly different size and body-mass structures. Three major questions will be addressed in the course of this research. Do reefscape structures and fish populations show significant clusters and discontinuities? Do such textural frequencies change across reefscapes and are they statistically equivalent within similar physiographic reef zones? If so, are fish body-size and mass clusters related to dominant textural frequencies of specific reef environments or to other causes?

Analysis of the fish population data will be developed in five stages. First, the textural framework for the analysis will be established using various site-specific physical characteristics contained in the NMFS database. Second, reef-fish community profiles will be developed and compared between homogeneous bottom-cover types and physiographic reef zones. Third, size characteristics of species, abundance and biomass will be developed and statistically compared between reefscapes. Fourth, cluster and gap analyses will be performed on species and size-specific body-mass data summed for specific bottom-cover classes. These will be compared for statistical consistency. Finally, the Textural-Discontinuity Hypothesis, the Limited Shelter Hypothesis and the three competing hypotheses will be evaluated based on results obtained in the previous sections and specific case studies.

Textural Analysis Framework

Given the relative absence of quantitative data on specific substrate textures, two approaches have been developed for evaluating the competing hypotheses: one based on qualitative bottom-cover categories and one based on quantitative surface-area estimates. First, fish sample sites containing 100 percent cover for each of the bottom-cover classes of coral, rubble, rock, grass and sand will be extracted from the database for comparative analysis. These bottom-cover classes represent a qualitative, but logical progression in substrate complexity as established in the literature. Second, surface-area estimates will be developed for coral, rock and rubble sample sites containing observations of local relief. Since surface area has been associated with geometric complexity, changes in fish-population characteristics will be analyzed across surface-area gradients, both within and between substrata. Where sample size permits, such analyses will be conducted for forereef and backreef environments as well as physiographic zones of individual reefs. Transition zones between the five generic classes will also be analyzed. If discontinuities and texture-related changes in fish body sizes do occur, then they should be evident between bottom-cover environments having such logical textural differences.

Reef-Fish Community Profiles

The second step in the analysis will be to construct basic statistical profiles for reef-fish communities in each bottom-cover class and physiographic reef zone or location and compare their characteristics. Species diversity, abundance, and biomass will be compiled using simple descriptive statistics. Zonal comparisons will be made using chi-square, one-way ANOVAs and standard similarity indexes. The purpose of this section is to confirm or contradict certain established paradigms in the literature concerning the productivity of specific reef environments and the general characteristics of coral-reef fish populations occupying different physiographic reef zones. This section will provide the background data for analyses to be conducted in later sections.

Fish Body-Mass Concentrations in Reefscapes

If fish body sizes cluster around the textural frequencies of reefscapes, then body mass clusters should be best developed around the dominant frequencies. These should change between substrata having very different geomorphic properties. Shifts in the dominant frequencies should result in corresponding shifts in size-specific concentrations of species and fish body mass. Cumulative frequency curves of species, abundance and biomass should reflect these size-specific concentrations, intervening gaps and shifts across reefscapes. Statistical comparisons using the Kolmorov-Smirnov (K-S) statistic should establish whether such curves vary significantly between reefscapes and whether they are statistically similar within them. Similarly, chi-square tests of percentage concentrations by length and weight groupings should detect significant shifts in aggregate body size to different frequencies. If the Textural-Discontinuity Hypothesis is correct, then cumulative frequency curves together with proportional length and weight concentrations should display statistical similarity between specific or random locations within any given bottom-cover class, and statistical differences between.

To test these assumptions, species, abundance and biomass measures will be computed in small length and weight increments directly from the species-specific observations contained in individual samples and normalized by sample size. Cumulative frequency curves and size groupings will be constructed from these aggregations. Similar data will be developed for individual samples and numerous random sub-samples selected from each bottom-cover class and compared using the chi-square, ANOVA, and K-S statistics.

Frequencies and Discontinuities

The fourth step in the analysis will be to establish whether specific body-mass frequencies and size-ordered discontinuities occur in fish populations occupying different physiographic reef zones, and whether they differ statistically within and between zones. In his analysis of birds and mammals of the boreal forests and short-grass prairies, Holling (1992) utilized species-specific adult body masses to test for discontinuities in the geometric properties of landscapes. Unlike birds and mammals, fish are characterized by indeterminate growth (Smith, 1978) and may have a wide range of adult body sizes in any one species. Species lengths at each of the study area sample sites represent the average of all individuals observed. Minimum and maximum values define the variance, but not the actual distribution. Thus, the mean length or biomass of any species computed across multiple samples in each bottom-cover class represents an average of means in measurements that have already been rounded to the nearest 1 cm. While preliminary analysis indicates that some species display narrow size ranges in means computed across samples in specific environments, many others are widely dispersed or multi-modal. Means computed from multi-modal distributions do not reflect the actual size frequencies of the population. Similarly, gaps may result simply from the utilization of means when, in fact, the distributions of species overlap.

Two statistical techniques will be used to identify any dominant frequencies and discontinuities that may occur in fish body-mass distributions within and across reefscapes and sample strata. The first technique may be referred to as a 'body-mass difference index' and is very similar to the one employed by Holling (1992). It produces a measure of the distance between elements in a size-ordered progression based on a split moving window ratio which is expressed as, $DI = 1 - ((S_n + S_{n-1}) / (S_n + S_{n+1}))$, where 'n' is equal to the rank-ordered observation and 'S' equals species-specific weight. It is used to identify discontinuities or 'gaps' between species clusters. The second technique utilizes a 'rolling regression' procedure to locate major breaks in the slope of log relationships between numerical fish properties such as specie occurrences or abundance and fish body weight. This procedure is based on the proposition that fish abundance should display a power relationship to fish size across fractal portions of the reefscape. Such relationships appear to be straight lines when plotted as log-log functions. Major breaks in the slope of the regression line are assumed to represent scale-specific discontinuities in the body-mass characteristics of fish populations.

Hypothesis Testing

The preceding analyses should provide most of the results necessary for testing the four hypotheses. If any of the competing hypotheses explain the occurrence and magnitude of body-size clusters, then any existing clump structure together with shifts within and between reefscapes should reflect distributions and changes in one or more of these variables. If random processes account for body-size clumps, it would seem unlikely that there would be any statistical consistency in fish body-mass distributions across similarly-structured reefscapes. Species size distributions and existing discontinuities should occur as random patterns. To test this proposition, random and location-specific subsamples will be extracted from the homogeneous bottom-cover samples and compared for statistical consistency. If body-mass size structures are statistically similar within specific substrata, then the stochastic null hypothesis cannot be rejected.

If fishes have a range of sizes that are related to the size of their food sources, then clusters and gaps could reflect 'standing waves' of size groupings that are dominated by particular trophic classes (Holling, 1992). Shifts in size structure might result from changes in the proportional concentrations of trophic groups as food sources change between bottom-cover types. It has been shown, for example, that certain types of plankton occur in greater concentrations over coral reefs than in surrounding waters. Similarly, macroalgae communities may have greater proportional densities in rock and rubble environments. To test this hypothesis, the size and mass characteristics of all trophic groups will be developed and compared for the five homogeneous bottom-cover types using the same battery of statistical tests employed in previous sections. If size-structure shifts are independent of changes in trophic concentrations, then this null hypothesis cannot be rejected.

The Dominant-Species Hypothesis has similarities to the preceding arguments. If a small number of successful species account for a large proportion of occurrences and abundance in particular habitats, then size-structure changes between bottom-cover types may reflect differences in the mix of successful species between habitats and not substrate characteristics. To test this hypothesis, all previously-defined fish-population characteristics will be recompiled and compared for dominant and non-dominant species in each of the five homogeneous substrata. If intersubstrate changes in size structure are independent of changes in the mixture of dominant species, then this null hypothesis cannot be rejected.

If the Textural-Discontinuity and Limited Shelter Hypotheses are correct then coral-reef landscapes and their resident fish populations should display scale-specific textural clusters or frequencies which are organized around a small set of structuring processes which change across scales at specific sites and within scales across the reef. These organizational patterns should be identifiable in the size-ordered progression of fish population body sizes and in the magnitudes of body mass, which develop within the clusters. Size-specific body-mass concentrations should recur with some consistency across reefscapes having similar structural characteristics. Such clusters should not be dominated by particular species or trophic classes, but should contain a mixture of species and trophic classes with similar-sized home ranges that exploit resources with similar spatial frequencies. As landscape assemblages change, so should the dominant textural frequencies and their magnitudes. Fish population clusters should display statistically consistent, size-specific changes in abundance and mass which reflect this shift in the dominant textural frequencies between reef landscapes. For example, whole clusters would be expected to disappear in the structural shift that occurs between coral and sand substrata.

CHAPTER 4
RESEARCH RESULTS

This chapter is organized into three major areas composed of 13 separate sections. The first two sections quantify the results of the sample-selection process and establish the relationships between the physical descriptors of substrate types contained in the database and their geometric properties, which are important to the analysis. The next six sections develop the statistical profiles and comparisons of community characteristics and population size structures for five homogeneous bottom-cover types and evaluate whether significant size-ordered discontinuities occur in fish populations occupying habitats having different geometric characteristics. These results are summarized into a set of statistical parameters that may be used to predict fish-population characteristics within the reef system based on the morphology or geometry of the substrata. The final five sections evaluate the primary and competing hypotheses using results from the previous sections and specific case studies developed from the database.

Study Area Sample Site Classification and Geographic Distribution

Analyses contained in this study are based on three sets of samples. The first set is composed of sample sites whose substratum was classified as homogeneous, i.e., comprised of 100-percent coral, rock, rubble, grass or sand. These samples are used for comparing fish-population characteristics between bottom covers having very different physical or geometric characteristics. The second set is composed of sample sites classified as pure mixtures (100-percent cover) of sand-coral, sand-rock, sand-rubble and sand-grass. These sites are used for evaluating changes in fish-population characteristics that occur in the transition between low and high-complexity, homogeneous bottom-cover types. The third set is composed of all sample sites containing observations of maximum local relief. These sites are used for evaluating trends in fish population characteristics that may be related to changes in gross, substrate surface area.

Substrate Classification

The National Marine Fisheries Service (NMFS) database contains 22 unique bottom-type classes whose combination describes the substrate characteristics of each of the 3,693 study-area sample sites. Summation of percentages for all 22 classes always equals 100 for each sample site. Coral, rock, rubble, grass and sand substrate components were developed by selecting specific classes to be assigned to each of the five homogeneous substrate types and adding the percentages for each sample site. This was done in consultation with Dr. James Bohnsack and Mr. Douglas Harper at the NMFS. Table 4.1 shows how each class was assigned and the number of occurrences within the database. Coral substrata are comprised of one generic and five specific coral classes. Soft corals (gorgonians) were excluded from this initial assignment. Grass and sand substrata include one and two classes respectively. Rock substrata include two classes, the first of which (platform) is comprised of exposed Holocene carbonates that are often referred to as 'hardbottom'. Other rock types include dead coral structures and substratum exposed as a result of natural and man-made events such as the

Table 4.1. Bottom-type classes, data base occurrences and substratum assignment.

Bottom Type	Coral	Rock	Rubble	Grass	Sand	Other
Coral	2910					
Wall						341
Platform		501				
Branching Coral (Acropora palmata)	383					
Branching Coral (Acropora cervicornis)	97					
Sand					2193	
Sand/Rubble			254			
Other (unknown)						378
Small Rubble			656			
Large Rubble			304			
Large Coral Heads	158					
Soft Corals (Gorgonians)						1857
Overhangs						101
Open Water						23
Fire Coral	445					
Coarse Sand					1	
Sea Grasses				293		
Massive Corals (Diploria)	34					
Rock		799				

Table 4.2. Sample sizes for homogeneous bottom-cover types by location.

	Biscayne Nat. Park Reefs	Looe Key Reef	Molasses Reef	Other Reefs	Total
All Coral	30	44	36	25	135
Forereef	4	43	36	13	96
Backreef	26	1	0	9	36
Deep Reefs	0	0	0	3	3
All Rock	2	5	19	5	31
Forereef	0	1	19	1	21
Wellwood (Shipwreck)	0	0	18	0	18
Backreef	2	4	0	1	7
Deep Reefs	0	0	0	3	3
All Rubble	0	10	27	4	41
Forereef	0	2	27	0	29
Wellwood (Shipwreck)	0	0	22	0	22
Backreef	0	8	0	4	12
All Grass	0	40	0	1	41
All Sand	0	9	0	12	21

grounding of the freighter M/V Wellwood. Rubble is comprised of three classes and represents a range of sizes extending from large pieces to mixtures of sand and small rubble. It is the only substrate type whose constituent class names contain specific geometric properties.

Sample Sizes and Geographic Distribution

Of 3,693 sample sites in the study-area database, only 266, or approximately 7 percent, were classified as homogeneous. Of this total, 135 or 50 percent were coral, 31 were rock, 41 were rubble, 41 were grass and 21 were sand (Table 4.2). Technically, homogeneous classes should include only sites containing 100 percent cover of a particular substrate type. In reality, such homogeneity is rare, and relative only at particular observation scales. Such sites represent the extremes in an otherwise more heterogeneous environment. This is particularly true in rubble substrata that usually include some sand. For this study the homogeneous rubble category has been defined to include the NMFS bottom-type class defined as sand/rubble (Table 4.1) and all sample sites containing a homogeneous mixture of rubble and sand, where the sand component is less than 10 percent (Table 4.2 and 4.3).

The homogeneous sample sites are geographically dispersed among several reef areas and zones (Table 4.2). Coral sample sites display the most even geographic dispersion, with 30 sites in Biscayne National Park, 47 sites at Looe Key Reef, 36 sites at Molasses Reef and 22 sites in other locations. Forereef-backreef locations were more clustered. Looe Key and Molasses Reef sites comprised 99 percent of forereef locations while 72 percent of backreef coral sites occurred in Biscayne National Park. Approximately 60 percent of homogeneous rock and rubble sites are located at the grounding site of the freighter M/V Wellwood on

Table 4.3. Number of sample sites containing homogeneous mixtures of sand-coral, sand-rock, sand-rubble and sand-grass.

Percentage coral, rock, rubble or grass	Forereef Sand-Coral	Backreef Sand-Coral	Sand-Rock	Sand-Rubble	Sand-Grass
5-19 percent	1	1	3	3	11
20-29 percent	4	3	2	0	4
30-39 percent	5	5	0	2	3
40-49 percent	18	9	1	0	2
50-59 percent	43	27	0	1	6
60-69 percent	57	19	1	4	3
70-79 percent	66	24	2	1	1
80-89 percent	67	17	1	10	2
90-99 percent	61	42	3	21	3
100 percent	96	36	31	20	41

Table 4.4. Sample sites with observations of maximum local relief. Sand and dominant coral-gorgonian mixtures include all sites where coral-gorgonian proportions are greater than rock-rubble proportions.

	Homogeneous Sand-Coral Sample Sites			Homogeneous Sand-Rock Sample Sites	Sand and Dominant Coral-Gorgonian Mixtures
Percentage Coral	Forereef	Backreef	Total		
5-19 percent	3	4	7	0	0
20-29 percent	3	3	6	3	3
30-39 percent	4	11	15	4	12
40-49 percent	14	6	20	2	33
50-59 percent	10	8	18	4	73
60-69 percent	11	6	17	0	81
70-79 percent	10	3	13	4	78
80-89 percent	7	1	8	4	50
90-99 percent	5	2	7	2	37
100 percent	11	0	11	3	34
Total	78	44	122	26	401

Molasses Reef. Homogeneous grass sites are almost all located at Looe Key while sand sites are nearly evenly split between Looe Key and other locations.

Sample sites containing mixtures of sand and one other substrate type are more numerous than homogeneous sites for coral and rubble substrata but less numerous in rock and grass (Table 4.3). There are 483 sites classified as pure sand-coral mixtures (13 percent of all samples) as compared to 12 for sand-rock, 42 for sand-rubble and 35 for sand-grass. Large majorities of these sample sites contain 50 percent or more of the more-complex substrate type. Given the small number of sample sites for mixtures of sand-rock and sand-rubble, a combined set of samples containing 100 percent mixtures of sand, rock and rubble was also created. This set contains 54 mixed sample sites and 51 homogeneous rock-rubble sites.

The third set of samples is composed of 649 sites containing observations of maximum local relief. A total of 122 of these sites are classified as homogeneous sand-coral mixtures, while 26 contain homogeneous sand-rock mixtures (Table 4.4). An expanded set of 401 sample sites was selected for analyzing fish-population characteristic changes across coral surface-area gradients. This set includes all sites having observations of relief where the combined coral-gorgonian (hard coral and soft coral) proportions were greater than the combined rock-rubble proportions. Sample sites containing more than 20 percent of their cover classified as something other than coral, gorgonian, rock, rubble, grass or sand were excluded from this subset.

The Physical Characteristics of Substrate Types

The literature suggests that substrate morphology as well as structure size and height are major factors affecting surface area and associated shelter characteristics in coral-reef environments. Dahl's analysis of theoretical reef surfaces indicated that feature height and frequency were the most important determinants of surface area (Dahl, 1973). Only qualitative measures of substrate morphology are available from the NMFS database. These include proportion bottom cover by type but no surface-area measures of the individual types. However, some quantitative measures of maximum local relief (height) are available for 649 sample sites. Of this total, 122 sites were classified as pure sand-coral mixtures and 26 sites as pure sand-rock mixtures. No sand-rubble sites were coded by relief. Since the geometric characteristics of shelter spaces should be related to surface complexity, it is important to evaluate how this variable responds to changes in the qualitative measures (proportion bottom cover by type) being used in this study. To accomplish this, Dahl's surface-area analyses (Dahl, 1973) are replicated using variables from the NMFS database.

Gross Structure Size and Surface Area

It can be shown that crude, three-dimensional surface area increases directly with the proportion of complex bottom cover at any particular sample site. Surface-area measurements at this scale, which Dahl (1973) referred to as the 'gross reef morphology index', are measured in tens to hundreds of square meters and are related to the two-dimensional area of 'hard' bottom cover within the visual census cylinder and the height at which such cover stands above any surrounding sand or seagrass surfaces. They are also related to the frequency of such features within any sample area and other superimposed morphological features such as spurs and grooves. However, since such characteristics are not recorded in the database, they are ignored in this analysis.

While no direct measurement of structure size is recorded in the database, substrata classified as homogeneous must represent relatively large structures, at least the size of the visual census cylinder diameter (48 feet). Within the sampling cylinder, the two-dimensional area of such a structure is 168.2 square meters (1809 square feet). Bottom covers containing mixtures such as coral and sand may represent several smaller reefs or large coral heads surrounded by sand, or the edge of a larger structure. Such reference data are not recorded in the database making actual perimeter calculations very difficult. However, the gross, two-dimensional (horizontal) surface area of complex bottom cover at a sample site increases directly with its proportion of total horizontal area in the visual census cylinder (Table 4.6).

Analysis of maximum vertical relief for mixed sand-coral and sand-rock sample sites indicate a positive, nearly linear relationship between the proportion of coral or rock in the sample and mean substrate height, suggesting that gross, three-dimensional surface area also increases, on average, directly with proportion complex bottom cover (Table 4.6, Figures 4.1A and D). These averages, however, mask the great variation in height that occurs across this spectrum (Figure 4.1A and 4.1D). Local relief varies from 0.3 to 5.5 meters across sample sites containing 90 to 100 percent coral cover and from 0.5 to 3 meters for rock substrata. While maximum observed values tend to increase across the range, very small values are also present in each proportion category. Regressions of individual sample sites yield very low correlation coefficients of 0.078 and 0.065 respectively but higher values of 0.81 and 0.29 for mean relief in 10 percent bottom-cover increments.

Maximum local relief may or may not be related to structure size, depending on the scale of the observation in relation to the structure. For example, a maximum relief of 0.3 meters (1 foot) recorded on the top of a very large patch reef or moderately-deep reef crest may say

Table 4.5. Analysis of variance: Mean relief by percent coral cover. Sample sites with one-foot local relief have been excluded. Numbers represent significant alpha levels below 0.20. NS equals 'not significant'.

Percent Coral Cover	Sample Size	Mean Relief (m)	5-29%	30-39%	40-49%	50-59%	60-69%	70-79%	80-89%	90-99%	100%
5-29%	12	0.58		0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
30-39%	15	1.10	0.01		NS	NS	0.01	0.03	0.01	0.02	0.01
40-49%	21	1.31	0.01	NS		NS	0.15	NS	0.02	0.04	0.01
50-59%	18	1.34	0.01	NS	NS		0.19	NS	0.02	0.05	0.01
60-69%	17	1.65	0.01	0.01	0.15	0.19		NS	0.13	0.15	0.05
70-79%	10	1.71	0.01	0.03	NS	NS	NS		NS	NS	0.15
80-89%	6	2.20	0.01	0.01	0.02	0.02	0.13	NS		NS	NS
90-99%	4	2.53	0.01	0.02	0.04	0.05	0.15	NS	NS		NS
100%	7	2.59	0.01	0.01	0.01	0.01	0.05	0.15	NS	NS	

Table 4.6. Surface-area index calculations for theoretical sample sites based on percent complex bottom cover, relief and object-specific surface-area indexes published by Dahl (1973). Massive, branched and plate-like coral-colony surface-area indexes were 1.4, 3 and 5.6 respectively. Categories a, b and c represent equal proportions of the named form types.

Percent Complex Bottom Cover	0%	10%	20%	30%	40%	50%	60%	70%	80%	90%	100%
1. Horizontal surface area (sq. meters)	168.2	168.2	168.2	168.2	168.2	168.2	168.2	168.2	168.2	168.2	168.2
a. Complex Surface Area	0	16.82	33.64	50.46	67.28	84.1	100.92	117.74	134.56	151.38	168.2
b. Sand Surface Area	168.2	151.38	134.56	117.74	100.92	84.1	67.28	50.46	33.64	16.82	0
2. Perimeter of contiguous complex horizontal surface (meters)	0	14.54	20.56	25.18	29.08	32.51	35.61	38.47	41.12	43.62	45.97
3. Mean relief (meters)	0	0.46	0.76	1.1	1.31	1.34	1.65	1.71	2.2	2.53	2.59
4. 3-dimensional complex surface (2 * 3 + 1a)	0	23.47	49.31	78.1	105.4	127.71	159.55	183.41	224.82	261.75	287.34
5. Gross reef morphology index - Scale I (4 ÷ 1a)	0	1.4	1.47	1.55	1.57	1.52	1.58	1.56	1.67	1.73	1.71
6. Coral colony or rubble index (Scale II)											
a. Massive/Branched/Plate Form index	3.34	3.34	3.34	3.34	3.34	3.34	3.34	3.34	3.34	3.34	3.34
b. Massive/Branched Form Index	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2	2.2
c. Massive Form index	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4	1.4
7. Scale I and II Index (6 times 5)											
a. Massive/Branched/Plate Form index	0	4.66	4.9	5.17	5.23	5.07	5.28	5.2	5.58	5.78	5.71
b. Massive/Branched Form Index	0	3.07	3.22	3.4	3.45	3.34	3.48	3.43	3.68	3.8	3.76
c. Massive Form index	0	1.95	2.05	2.17	2.19	2.13	2.21	2.18	2.34	2.42	2.39
8. Combined surface area index (6 * 4 + 1b) / 1											
Scale I Surface-Area Index	1	1.04	1.09	1.16	1.23	1.26	1.35	1.39	1.54	1.66	1.71
Massive-Branched-Plate Index (Scale I-II)	1	1.37	1.78	2.25	2.69	3.04	3.57	3.94	4.66	5.3	5.71
Massive-Branched Index (Scale I & II)	1	1.21	1.44	1.72	1.98	2.17	2.49	2.7	3.14	3.52	3.76
Massive Index (Scale I & II)	1	1.1	1.21	1.35	1.48	1.56	1.73	1.83	2.07	2.28	2.39
Large-Dense Rubble Index (Scale II)	1	1.08				2.5					4.27

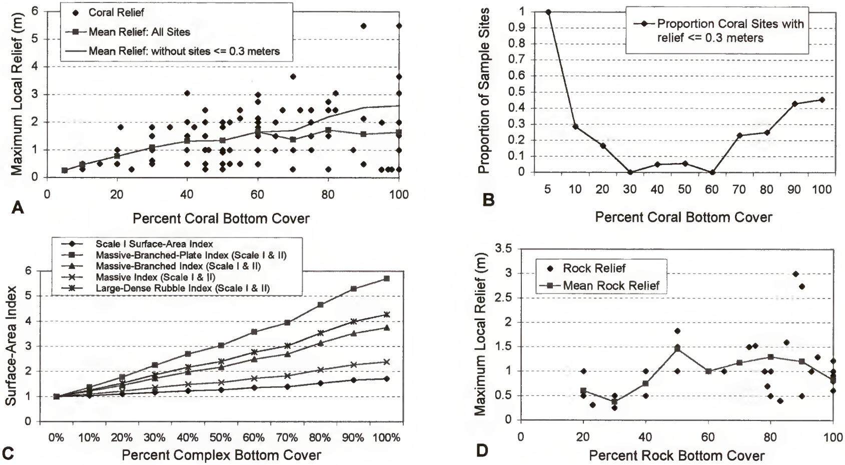

Figure 4.1. Relationships between substrate relief or surface area and percent bottom cover for sand-coral and sand-rock substrata. A) Relationship between percent coral and maximum local relief. B) Proportion of mixed sand-coral samples with relief <= 0.3 meter. C) Surface-area indexes by geometric surface type. D) Relationship between percent rock and maximum local relief.

nothing about the actual relief of the structure in question. Such observations may be spurious as they are related to the size of the observation cylinder, which is smaller than the structure. This observation is supported by the data. Sample sites having a maximum relief of 0.3 meters or less decline from 100 percent of all sites at 5 percent coral cover to 0-5 percent at sites containing 30 to 60 percent coral and then steadily increase to just under 50 percent at 100 percent coral cover (Figure 4.1B). Furthermore, all of the latter sites occur in the forereef zone, which typically has larger structures. Removal of these sites from the analysis results in a more-linear relationship between relief and percent coral cover (Figure 4.1A). While variation between coral sample sites remains large, correlation coefficients increase to 0.29 for individual sites and 0.98 for mean relief in 10 percent bottom-cover increments. One-way ANOVAs computed across individual sample sites show no significant difference in mean relief between pairings of adjacent bottom-cover categories. However, these values become significant beyond two or three adjacent categories (Table 4.5). Mean relief values for sites containing 5 to 29 percent coral are significantly different from all other categories, while homogeneous coral sites have significantly greater relief than all categories less than 80 percent cover.

Larger-Scale Geometric Properties and Surface Area

Superimposed on these smaller-scale surfaces are the larger-scale geometric forms of coral colonies, detrital materials and detailed rock surfaces. These are the scales at which fishes feed and seek shelter. Dahl (1973) published surface-index (SI) estimates for massive (SI=1.4), branched (SI=3.0) and plate-like or ridged (SI=5.6) coral forms as well as rubble of various sizes and densities (SI=1.08 to 2.5). A simulation of this range in total surface area and index values that result from various combinations of geometric forms of similar relief is shown in

Table 4.6 and Figure 4.1C. Three coral-morphology combinations were constructed from equal proportions of massive/branched/plate, massive/branched and massive only (Table 4.6). The first represents a mixture of morphologies characteristic of high-energy forereef environments, while the latter more closely represents low-energy backreef locations. Results suggest that differences in morphology between homogeneous forereef and backreef coral sites may result in surface-area differences of up to 250 percent (Table 4.6, Figure 4.1C). Surface-area comparisons for rubble substrata can be generated from Dahl's measurements of rubble surfaces where indexes ranged from 1.08 to 2.5. From his descriptions, I have estimated that the proportion of rubble at these sites ranged from 10 to 50 percent with the latter having greater relief than the former. Extrapolation of these indexes suggests that total surface area at homogeneous rubble sites may be comparable with the middle range in coral estimates.

The combined surface-area index (Table 4.6, Figure 4.1C) shows that total surface area at any sample site is dependant upon three factors: the proportion of horizontal area occupied by complex substrata, substrate height or relief, and the morphological characteristics of the larger-scale surface. Of these components, the latter is the most important, accounting for the vast majority of variation in the index. Such indexes, however, do not provide a measure of cavity sizes that occur in substrata composed of different geometric elements. While total available shelter should increase with surface area, the geometric characteristics of such spaces cannot be analytically defined from the existing data. However, visual assessments of such environments leave little doubt that the geometric elements and spaces in coral substrata cover a wider range and are much larger on average than those in rock, rubble, grass and sand bottom covers. Furthermore, as structures become larger and higher, it is probable that the range and median size of elements and spaces increase. A fractal analysis of such characteristics developed from theoretical assemblages, field measurements or digital images could provide analytical support for such a thesis, but is outside of the scope of this study.

Species Characteristics and Comparisons for Homogenous Substrate Types

Fish species diversity, as measured by mean species per sample, increases by more than one order of magnitude across the sand-to-coral complexity gradient (Table 4.7). The absolute number of species observed in any specific bottom-cover type is a function of sample size. As the number of samples increase (decreasing scale), so do the number of recorded species. While the mean number of species for individual sample sites ranges from 1.6 for sand to 21.3 for rubble, the average number of species observed in 31 sample sites ranges from 16 for sand to 98 for rubble (Table 4.7). Sand bottom-cover samples contain, on average, very few species of relatively small size. Species diversity in grass bottom covers increases by a factor of three but size remains relatively small. Diversity in rock, rubble and coral bottom covers are nearly 4 times those of grass and 12 to 13 times those of sand for individual sample sites. One-way ANOVAs computed across substrate-specific samples indicate that all sample pairings of the more-complex bottom covers with grass and sand are significantly different at or above the 0.01 confidence level (Table 4.8). Pairings of the more-complex substrata show no significant difference in mean number of species between coral and rubble sample sites. Rock substrata display mixed results. While means for individual sample sites contain 9 percent fewer species than coral or rubble and are significantly different at the 0.06 and 0.03 levels respectively, the mean number of species observed in 31 randomly-selected coral and rubble sample sites display no significant differences from rock samples (Table 4.7).

Table 4.7. Species characteristics for homogeneous bottom-cover types.

	All Coral	All Rock	All Rubble	All Grass	All Sand
Sample Size	135	31	41	41	21
Mean Species Per Sample	20.8	18.9	21.3	5.1	1.6
1-9.9 cm	8.2	10.3	12.6	3.7	1.3
10-19.9 cm	8	5.4	5.3	0.5	0.1
20+ cm	4.6	3.2	3.4	0.9	0.2
Median Species Per Sample	21	19	22	5	1
Mean Fish Length (cm)	14	12.6	11.7	11.3	9.7
Median Fish Length (cm)	11	8.2	7.5	5.1	4.9
Proportion Species by Length Group					
All Lengths	1	1	1	1	1
1-9.9 cm	0.395	0.544	0.59	0.719	0.794
10-19.9 cm	0.384	0.287	0.249	0.1	0.088
20+ cm	0.221	0.169	0.162	0.181	0.118
Median Fish Weight (grams)	34	12.3	9.8	2.4	1.5
Mean Species Per Sample by Fish Weight					
Less than 1 gram	1.3	1.5	3.2	1.6	0.4
1 to 10 gram	4.9	6.9	7.5	2	0.8
10 to 100 grams	8.9	6.6	6.7	0.6	0.2
100 to 1000 gram	5.2	3.2	3.2	0.7	0.1
1000 plus gram	0.5	0.6	0.7	0.3	0.1
Proportion Species by Fish Weight					
Less than 1 gram	0.061	0.08	0.151	0.319	0.265
1 to 10 gram	0.234	0.368	0.353	0.386	0.471
10 to 100 grams	0.428	0.352	0.314	0.11	0.118
100 to 1000 gram	0.252	0.168	0.151	0.129	0.088
1000 plus gram	0.025	0.032	0.031	0.057	0.059
Total Species (31 random sample sites)	93	93	98	43	16
Coral Shared Species		71	72	32	5
Rock Shared Species	71		72	32	7
Rubble Shared Species	72	72		35	10
Grass Shared Species	32	32	35		9
Sand Shared Species	5	7	10	9	
Unique Species	9	11	12	3	4
Unique Species Per Sample	0.7	0.4	0.5	0.1	0.5

Table 4.8. Significance levels of statistical tests of species for homogeneous bottom-cover types. Numbers represent significant alpha levels below 0.20. NS equals 'not significant'.

Chi-square Tests: Proportion Species by Length Group	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.11	0.03	0.01	0.01
All Rock	0.11		NS	0.02	0.01
All Rubble	0.03	NS		0.03	0.01
All Grass	0.01	0.02	0.03		NS
All Sand	0.01	0.01	0.01	NS	
K-S Tests: Cumulative Frequency of Species by Fish Length	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		NS	0.09	0.01	0.01
All Rock	NS		NS	0.02	0.01
All Rubble	0.09	NS		0.15	0.09
All Grass	0.01	0.02	0.15		NS
All Sand	0.01	0.01	0.09	NS	
One-Way ANOVA Tests: Mean Species Per Sample (All Sites)	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.06	NS	0.01	0.01
All Rock	0.06		0.03	0.01	0.01
All Rubble	NS	0.03		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	
One-Way ANOVA Tests: Mean Species Per Sample (31 random sample sites)	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		NS	NS	0.01	0.01
All Rock	NS		NS	0.01	0.01
All Rubble	NS	NS		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	
One-Way ANOVA Tests: Mean Fish Length (cm) Per Sample	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.05	0.01	0.05	0.03
All Rock	0.05		NS	NS	NS
All Rubble	0.01	NS		NS	NS
All Grass	0.05	NS	NS		NS
All Sand	0.03	NS	NS	NS	

There is a common pool of species that are found in multiple bottom-cover types and account for the vast majority of total species occurrences. Only a small proportion of this regional faunal pool is found at any individual sample site. The complex bottom covers share the greatest number of species (Table 4.7). These account for over 95 percent of all species occurrences. Substrate-specific unique species are, with few exceptions, rare and account for less than 5 percent of all occurrences. However, they account for 10 to 12 percent of all species found in coral, rock and rubble bottom covers, and 25 percent of all species observed at sand sample sites (Table 4.7).

Species similarity indexes computed for homogeneous substrate pairings measure both the increase in species numbers that occur across the habitat-complexity gradient as well as shifts in specie assemblages. The proportion of shared species between pairings (Table 4.9) appears to be a function of structural complexity, as assemblage similarity consistently decreases across the gradient. The proportion of shared species and similarity index values are greatest between bottom covers whose structural complexity are adjacent along the gradient and least at opposite ends of the gradient. Similarity indexes are computed from a modified version of Schoener's index of niche overlap (Gladfelter et al., 1980) and is expressed as $d = 1 - (\sum|x_i - y_i| / \sum |x_i + y_i|)$, where x and y represent site-specific occurrence values for each species in the assemblage. They weigh not only the presence or absence of species between samples but also their relative proportion of total species occurrences. Results indicate that similarity between samples is much greater within bottom-cover classes than between (Table 4.9, Figure 4.4D). While similarity is greatest between the more-complex substrate types (coral, rock and rubble), between-class values are significantly different than within-class values based on species-specific occurrences. Similarity between pairings also increases with sample

Table 4.9. Species similarity indexes for homogeneous bottom-cover types constructed from 10 random samples of 10 sites each (Part A) and 1 site each (Part B). Proportion shared species are computed by dividing cell-specific shared species by total species for each row. Similarity indexes are computed from a modified version of Schoener's Index of Niche Overlap published by Gladfelter et al. (1980).

Part A: 10 Random Samples of 10 sites each.	All Coral	All Rock	All Rubble	All Grass	All Sand
Total Species	96.5	92.5	103.5	41.5	16
Proportion Shared Species					
All Coral	0.984	0.762	0.808	0.337	0.052
All Rock	0.795	0.995	0.811	0.346	0.076
All Rubble	0.754	0.725	0.986	0.343	0.097
All Grass	0.783	0.771	0.855	0.964	0.205
All Sand	0.313	0.438	0.625	0.531	1
Modified Schoener's Index of Niche Overlap					
All Coral	0.926	0.713	0.69	0.217	0.029
All Rock	0.713	0.94	0.787	0.271	0.041
All Rubble	0.69	0.787	0.921	0.289	0.048
All Grass	0.217	0.271	0.289	0.924	0.202
All Sand	0.029	0.041	0.048	0.202	0.848
Part B: 10 Random Samples of 1 site each.	All Coral	All Rock	All Rubble	All Grass	All Sand
Total Species	59	61.5	61	19.5	5.5
Proportion Shared Species					
All Coral	0.864	0.674	0.754	0.195	0.038
All Rock	0.646	0.829	0.715	0.199	0.053
All Rubble	0.73	0.721	0.852	0.238	0.041
All Grass	0.59	0.628	0.744	0.462	0.154
All Sand	0.409	0.591	0.455	0.545	0.545
Modified Schoener's Index of Niche Overlap					
All Coral	0.761	0.609	0.636	0.133	0.021
All Rock	0.609	0.798	0.711	0.197	0.038
All Rubble	0.636	0.711	0.84	0.215	0.027
All Grass	0.133	0.197	0.215	0.522	0.188
All Sand	0.021	0.038	0.027	0.188	0.64

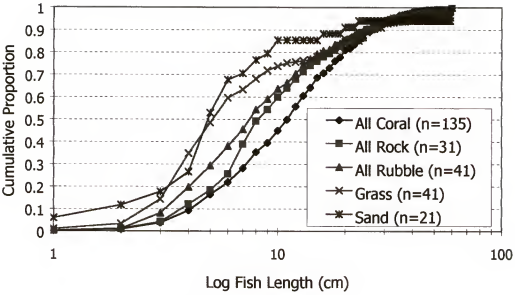

Figure 4.2. Cumulative frequency of all species by fish length for homogeneous bottom-cover types.

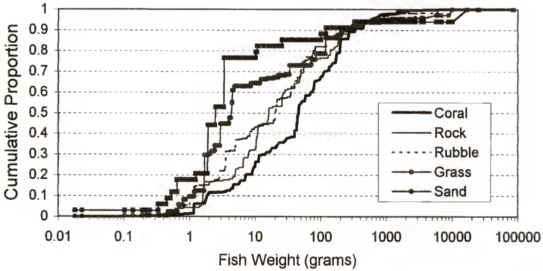

Figure 4.3. Cumulative frequency of all species by fish weight for homogeneous bottom-cover types.

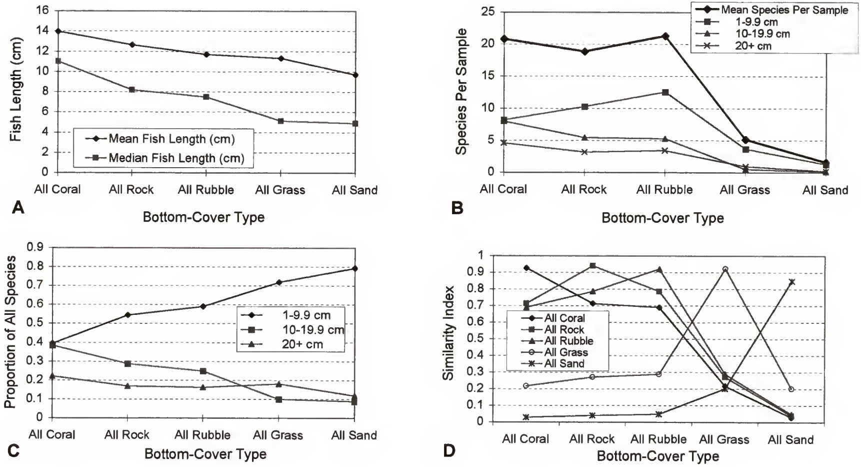

Figure 4.4. Species length characteristics and similarity indexes for homogeneous bottom-cover types. A) Mean and median fish lengths. B) Mean species per sample: total and by length grouping. C) Species proportions by length grouping. D) Similarity indexes within and between bottom-cover types.

size. Thus, the mean values obtained for ten random samples of ten sites each have within-class index values ranging from 0.85 to 0.94 for the 5 homogeneous substrate types while ten random samples of one site each range from 0.52 to 0.84 (Table 4.9). The greatest difference occurs in bottom covers having the fewest species (grass and sand) and, thus, the greatest variance between sample sites. In all tested cases, these are significantly larger than between-class pairings.

Species values decrease in a series of two or three significant steps across the complexity gradient depending on the statistic used. While mean species comparisons indicate two steps (Table 4.7 and Figure 4.4B), similarity indexes suggest three (Table 4.9 and Figure 4.4D). The transition from coral to rock and rubble substrata form one distinct step when measured by similarity indexes but are nearly identical in terms of mean species per sample. In other words, while the total number of species is not significantly different between these three substrate types, the proportional distribution of species occurrences within the assemblages are significantly different. The largest step in this transition occurs between the more complex substrata (coral, rock and rubble) and grass bottom covers. Grass bottom covers have unique characteristics in this hierarchy. While 77 to 85 percent of grass fish species are also observed in coral, rock and rubble substrata, similarity indexes for grass pairings with all other bottom-cover types are virtually the same, ranging from 0.20 to 0.29 or 0.13 to 0.21 depending on the number of sample sites used in the similarity index (Table 4.9). Over 50 percent of all sand species are also found in grass substrata suggesting that grass may represent a transition habitat in the assemblage shift which occurs between low and high-complexity bottom covers. The second or third step in this transition is from grass to sand bottom covers. Both mean species and species similarity indexes are significantly different between grass and sand sample sites.

Species Size Structure

Fish species size, as measured in mean and median fish length in centimeters and median fish weight in grams, declines significantly across the complexity gradient. Mean fish length declines from 14 cm for coral samples to 12.6 cm for rock to 11.7 cm for rubble to 11.3 and 9.7 cm respectively for grass and sand (Figure 4.4A). One-way ANOVA results (Table 4.8) show statistically-significant differences for mean species length at or above the 0.05 confidence level for all substrate sample pairings with coral, but not for any other combination. This is the result of increasing variances about the mean, which are induced by larger-sized species outliers, which increasingly distort the mean as the size curves shift to smaller sizes. These outliers are evident in Figure 4.6. Median fish lengths are more indicative of the size shift that occurs across the complexity gradient. These shifts appear to occur as two distinct steps between three levels: sand-grass, rock-rubble and coral (Table 4.7 and Figure 4.4A). Shifts in median fish weight are even more dramatic. Species weights in rock and rubble substrata have median values which are 36 and 29 percent of coral weights respectively, while grass and sand weights are 7 and 4 percent of those found in coral (Table 4.7, Figure 4.5A).

These size shifts are evident in the concentration of species by length group and weight class. When compared for three fish-length categories (1-9.9 cm, 10-19.9 cm and 20-plus cm), there is an increasing concentration of species in the smallest length group and a coincident decline in larger-sized species across the coral-to-sand complexity gradient (Table 4.7, Figure 4.4C). Comparisons of five weight classes produce the same results. Species proportions increase in the 1-10 gram weight classes and decline in the 10-1000 gram weight classes (Table 4.7, Figure 4.5C). These changes occur in two steps that may correspond to sharp transitions

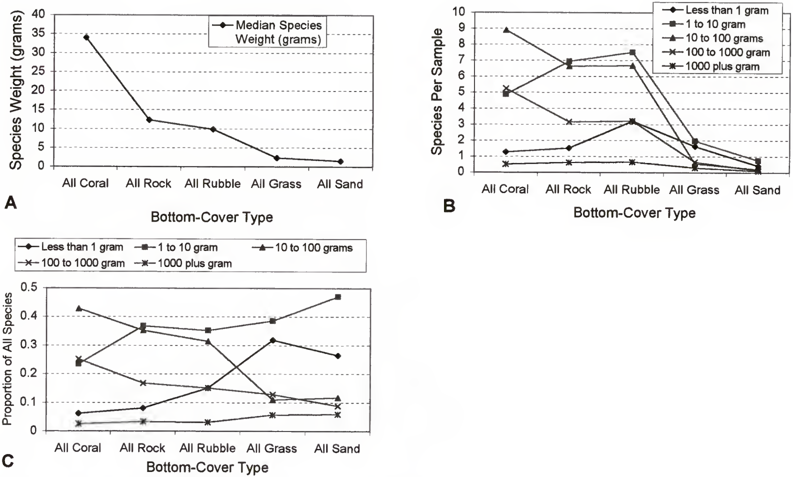

Figure 4.5. Species weight characteristics for homogeneous bottom-cover types.
A) Median species weight. B) Mean species per sample by weight grouping. C) Proportion of total species by weight grouping.

between three unique scales in reefscape geometry. Transition-step one is the shift from coral to rock and rubble bottom covers. Here, species diversity is nearly as great or slightly greater than in coral substrata (Table 4.7) but is disproportionately concentrated in smaller length groups and weight classes (Figure 4.4C, Figure 4.5C). Mean species per sample in the smallest grouping (1-9.9 cm) increase by 25 to 50 percent respectively while species in the larger groups (10-19 cm and 20-plus cm) decline, on average, by 32 and 24 percent. The second step in the transition, which occurs from rock-rubble to grass-sand, is precipitous with large absolute declines in all length and weight groups (Figures 4.4B and 4.5B) but large proportional increases in the smallest categories (Figures 4.4C and 4.5C). Here, coral substrata contain 57 times the number of species in the 10-19.9 cm length group as do sand substrata.

Statistical tests confirm these breaks between levels. Chi-square tests conducted on species percentages by length group (Table 4.8) indicate statistical independence for all sample pairings except rock-rubble and grass-sand. K-S statistics (Table 4.8) computed on cumulative frequency curves by fish length (Figure 4.2) show the same results. All sample pairings are significantly different at or above the 0.15 confidence level except coral-rock, rock-rubble and grass-sand. The coral-rock pairing is significant at the 0.21 level. Cumulative frequency curves by fish weight (Figure 4.3) are similar.

The Mechanics of Species Size-Structure Changes

The fundamental mechanics of these size shifts involve two interrelated processes: an absolute decline in the median weights and occurrences of specific species occupying the middle size ranges in coral bottom covers, and an increase in the occurrences of specific species in the smallest size ranges. Both processes result in a differential re-concentration of species (mean species per sample) into the smallest size groups in the transition from coral to other bottom covers (Figure 4.6). Figure 4.7 illustrates the median weight losses which occur for common (shared) species in the transition from coral to rock, rubble, grass and sand substrata. Such changes account for nearly one-third of the size shift in coral-rock and coral-rubble transitions (Table 4.10). Fully 65 percent of all shared coral species weighing from 10 to 300 grams have lower median weights in rock substrata, as compared to only 12 percent of shared species in other weight groups. In comparison, 66 percent of all species common to both coral and rubble substrata display median weight decreases, regardless of size. A similar phenomenon occurs in grass, where 95 percent of all shared coral species weighing less than 100 grams decline in weight.

Size-specific changes in species occurrences account for two-thirds of the size shift between complex bottom covers. Shared species in the middle weight ranges occur less frequently in non-coral bottom covers while those weighing less than 10 grams occur more frequently (Table 4.10). Unique species, which comprise only a small proportion of all occurrences, are dramatically stratified by size. While unique coral species cover a wide size spectrum with a median weight of 117 grams, unique rock and rubble species are overwhelmingly small, with median weights of 2.9 and 1.3 grams respectively (Table 4.10). Not a single unique rubble species occurs in the 10-to-300 gram weight range. In grass and sand bottom covers, the largest component of change is the loss of 50 and 90 percent respectively of all species occurring in coral substrata. However, shared species weight differences still account for a large component of change in grass bottom covers. Fifty percent of such species weighing from 10 to 300 grams in coral substrata display weight changes of one order of magnitude or

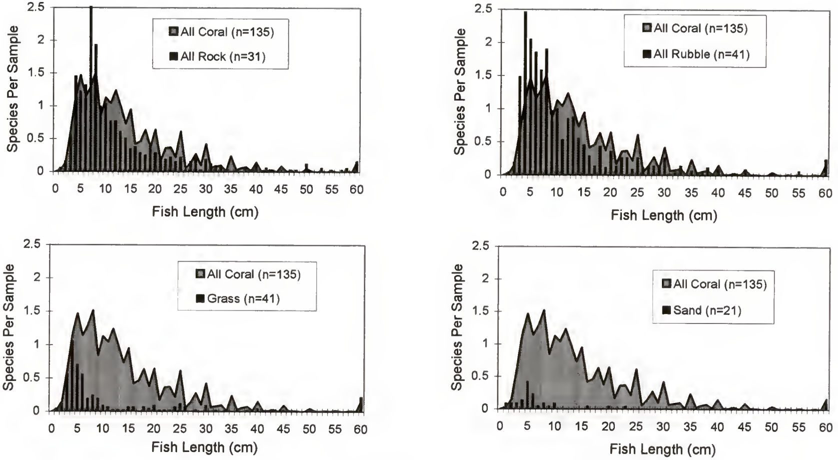

Figure 4.6. Species per sample distributions by bottom-cover type in 1-cm length increments. Species per sample were computed by aggregating all species at each sample site by bottom-cover type into 1-cm length increments and dividing by the sample size. Lengths beyond 60 cm are included in the 60-cm increment.

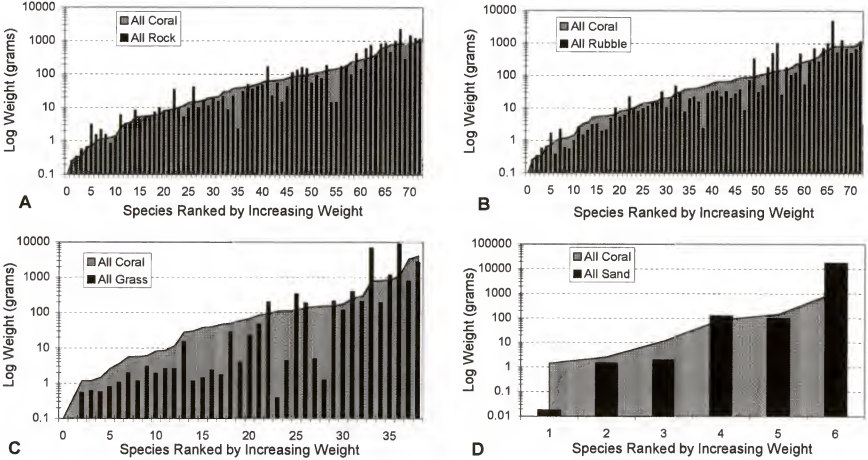

Figure 4.7. Species-specific median weights for common (shared) species for pairings of homogeneous substrata.

A) Species-specific weight changes for shared species between coral and rock substrata.

B) Species-specific weight changes for shared species between coral and rubble substrata.

C) Species-specific weight changes for shared species between coral and grass substrata.

D) Species-specific weight changes for shared species between coral and sand substrata.

Table 4.10. Components of species size change for homogeneous bottom-cover types. Common specie occurrence changes are calculated as the difference between the total occurrences of coral species remaining in the same weight category in the new substratum type minus the original values. Weight changes represent species-occurrence shifts between weight categories and always sum to zero.

	Common Species				Unique Species		
	Species Per Sample		Source of Change in Common Species Per Sample		Species Per Sample		
	Coral	Rock	Weight Changes	Occurrence Changes	Coral	Rock	Occurrence Changes
Less than 10 grams	5.33	8.29	1.03	1.93	0.07	0.42	0.35
10 to 99 grams	8.46	6.52	0.13	-2.07	0.41	0.06	-0.34
100 to 299 grams	3.54	1.71	-1.06	-0.77	0.81	0.06	-0.75
300-plus grams	1.44	1.29	-0.1	-0.06	0.25	0	-0.25
All Species	18.77	17.81	0	-0.96	1.54	0.55	-0.99
Median Weight	41.57	22.6			117.11	2.86	
	Coral	Rubble	Weight Changes	Occurrence Changes	Coral	Rubble	Occurrence Changes
Less than 10 grams	5.33	8.46	0.88	2.26	0.1	0.98	0.87
10 to 99 grams	8.46	7.46	0.15	-1.14	0.25	0	-0.25
100 to 299 grams	3.54	2.51	-0.44	-0.59	0.31	0	-0.31
300-plus grams	1.44	1.15	-0.59	0.29	0.39	0.12	-0.27
All Species	18.77	19.59	0	0.81	1.06	1.1	0.04
Median Weight	41.57	22.25			120.35	1.25	
	Coral	Grass	Weight Changes	Occurrence Changes	Coral	Grass	Occurrence Changes
Less than 10 grams	3.84	3.49	1.02	-1.38	1.61	0	-1.61
10 to 99 grams	4.3	0.32	-0.71	-3.27	4.6	0.12	-4.48
100 to 299 grams	2.36	0.68	-0.24	-1.43	1.9	0	-1.9
300-plus grams	0.52	0.39	-0.07	-0.06	1.64	0.05	-1.59
All Species	11.01	4.88	0	-6.14	9.76	0.17	-9.58
Median Weight	63.6	4.23			68.76	44.94	
	Coral	Sand	Weight Changes	Occurrence Changes	Coral	Sand	Occurrence Changes
Less than 10 grams	1.06	0.57	0.38	-0.87	4.4	0.62	-3.78
10 to 99 grams	0.01	0	-0.38	0.37	8.56	0.14	-8.41
100 to 299 grams	0.4	0.1	0	-0.3	4.19	0	-4.19
300-plus grams	0.13	0.1	0	-0.03	2.03	0.1	-1.93
All Species	1.59	0.76	0	-0.83	19.18	0.86	-18.32
Median Weight	48.54	51.58			68.03	1.38	

more in grass bottom covers (Figure 4.7). This observation supports the often-cited contention that seagrass habitats serve as 'nursery' areas for the juveniles of many reef species.

Species Transitions from Sand to Complex Substrate Types

Analysis of mixed bottom covers comprised of 100 percent sand-coral, sand-rock and sand-rubble indicate that mean species per sample increase directly with the proportion of complex bottom cover. As previously demonstrated, complex bottom-cover proportions are directly correlated with relief and gross morphological surface area. The mean number of species increases rapidly and then more slowly as incremental amounts of complex habitat are added to the environment (Table 4.11). These species diversity curves are not significantly different between coral and rock-rubble substrata (Figure 4.8A) as demonstrated by one-way ANOVAs (Table 4.12). Simple linear regressions computed for mean species per sample and proportion complex bottom cover in 10-percent increments resulted in R-square values of 0.76 and 0.59 respectively. Although there is great variation in species numbers between individual sample sites having the same complex bottom-cover proportion (Figures 4.8B and C), one-way ANOVAs suggest that the progression in mean values across this transition are significant (Tables 4.11 and 4.12).

Fish-specie assemblages in mixed bottom covers very rapidly assume the size structure of the more-complex substrate type in the mixture. Mixed sample sites having a low proportion of coral initially display a higher median species length due to a smaller concentration of species in the less-than-20 cm length groups (Table 4.11). While larger species increase at a lower rate than small and medium-sized species, all coral length groups show absolute increases across the transition. Beyond 19 percent coral cover, there are no significant differences in size structure

Table 4.11. Species characteristics across the transition from sand to coral and sand to rock/rubble environments. Column headers refer to the percentage of coral or rock/rubble in the sand-coral or sand-rock/rubble mixture. Statistical test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	5 to 19%	20 to 29%	30 to 39%	40 to 49%	50 to 59%	60 to 69%	70 to 79%	80 to 89%	90 to 99%	100%
Sand-Coral Sample Size	2	7	10	27	70	76	93	85	105	135
Mean Species Per Sample - Coral	9.5	14.7	15.7	18.8	18.8	20.9	20.5	21.9	20.8	20.8
1-9.9 cm - Coral	3.5	6.1	8.1	8.9	8.2	9.6	9.6	9.6	9.1	8.2
10-19.9 cm - Coral	2.5	5.6	4.3	5.9	6.8	7.3	7.1	8	7.5	8
20+ cm - Coral	3.5	3	3.3	4	3.8	4	3.7	4.4	4.2	4.6
Median Length (cm) - Coral	11.8	9.9	8.8	9.8	10.1	9.9	9.6	10	10.2	11
Proportion Species by Length Group										
1-9.9 cm - Coral	0.368	0.417	0.516	0.473	0.436	0.459	0.469	0.435	0.439	0.395
10-19.9 cm - Coral	0.263	0.379	0.274	0.316	0.364	0.348	0.348	0.365	0.361	0.384
20+ cm - Coral	0.368	0.204	0.21	0.211	0.2	0.193	0.183	0.199	0.2	0.221
Sand-Rock/Rubble Sample Size	6		5		8		20		33	63
Species Per Sample –Rock/Rubble	12.5		18.8		18.9		19.5		21.0	19.6
1-9.9 cm – Rock/Rubble	8.0		9.6		9.9		11.5		11.9	11.1
10-19.9 cm – Rock/Rubble	2.2		5.2		6.6		5.2		5.7	5.2
20+ cm – Rock/Rubble	2.3		4		2.4		2.8		3.4	3.3
Median Length (cm) – Rock/Rubble	6.6		8.8		8.6		7.4		7.6	7.9
One-Way ANOVA Tests: Sand-Coral Mean Species Per Sample	5 to 29%	30 to 39%	40 to 49%	50 to 59%	60 to 69%	70 to 79%	80 to 89%	90 to 99%	100%	
5 to 29%		NS	0.02	0.01	0.01	0.01	0.01	0.01	0.01	
30 to 39%	NS		0.12	0.1	0.01	0.01	0.01	0.01	0.01	
40 to 49%	0.02	0.12		NS	0.07	0.1	0.01	0.05	0.07	
50 to 59%	0.01	0.1	NS		0.02	0.03	0.01	0.01	0.01	
60 to 69%	0.01	0.01	0.07	0.02		NS	0.19	NS	NS	
70 to 79%	0.01	0.01	0.1	0.03	NS		0.11	NS	NS	
80 to 89%	0.01	0.01	0.01	0.01	0.19	0.11		NS	0.11	
90 to 99%	0.01	0.01	0.05	0.01	NS	NS	NS		NS	
100%	0.01	0.01	0.07	0.01	NS	NS	0.11	NS		

Table 4.12. Significance levels of statistical tests of species characteristics across the transition from sand to coral and sand to rock/rubble environments. Column headers refer to the percentage of coral or rock/rubble in the sand-coral or sand-rock/rubble mixture. Statistical test values represent significant alpha levels below 0.20. NS equals 'not significant'.

One-Way ANOVA: Sand-Coral Median Species Weight Per Sample	5 to 29%	30 to 39%	40 to 49%	50 to 59%	60 to 69%	70 to 79%	80 to 89%	90 to 99%	100%
5 to 29%		NS	0.12	0.03	0.01	0.01	0.02	0.01	0.07
30 to 39%	NS		NS	0.05	0.1	0.15	0.06	0.09	0.01
40 to 49%	0.12	NS		NS	NS	NS	NS	NS	0.01
50 to 59%	0.03	0.05	NS		NS	0.18	NS	NS	0.01
60 to 69%	0.01	0.1	NS	NS		NS	NS	NS	0.01
70 to 79%	0.01	0.15	NS	0.18	NS		0.16	NS	0.01
80 to 89%	0.02	0.06	NS	NS	NS	0.16		NS	0.01
90 to 99%	0.01	0.09	NS	NS	NS	NS	NS		0.01
100%	0.07	0.01	0.01	0.01	0.01	0.01	0.01	0.01	
One-Way ANOVA: Sand-Rock-Rubble Mean Species Per Sample	5 to 29%	30 to 49%	50 to 69%	70 to 89%	90 to 99%	100%			
5 to 29%		0.09	0.08	0.01	0.01	0.01			
30 to 49%	0.09		NS	NS	NS	NS			
50 to 69%	0.08	NS		NS	NS	NS			
70 to 89%	0.01	NS	NS		NS	NS			
90 to 99%	0.01	NS	NS	NS		0.16			
100%	0.01	NS	NS	NS	0.16				
Coral vs. Rock/Rubble	NS	NS	NS	NS	NS	0.11			
One-Way ANOVA: Sand-Rock-Rubble Median Species Weight Per Sample	5 to 29%	30 to 49%	50 to 69%	70 to 89%	90 to 99%	100%			
5 to 29%		NS	NS	NS	NS	NS			
30 to 49%	NS		NS	NS	NS	NS			
50 to 69%	NS	NS		NS	NS	0.17			
70 to 89%	NS	NS	NS		NS	NS			
90 to 99%	NS	NS	NS	NS		0.14			
100%	NS	NS	0.17	NS	0.14				

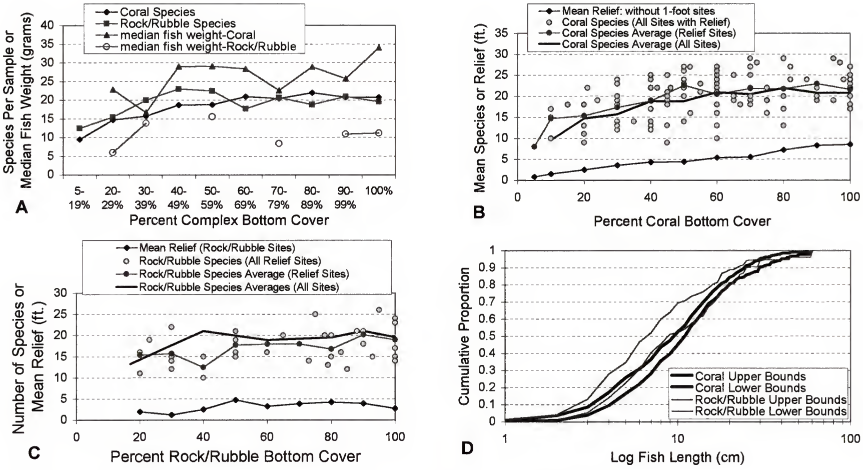

Figure 4.8. Species characteristics and comparisons across the sand-coral and sand-rock/rubble transition. A) Mean species per sample and median species weights in grams. B) Species numbers in mixed sand-coral bottom covers. Substrate relief is presented in feet for visual purposes. C) Species numbers in mixed sand-rock/rubble bottom covers. Substrate relief is presented in feet for visual purposes. D) Cumulative size ranges for mixtures of sand-coral and sand-rock/rubble.

detected by chi-square tests between homogeneous coral and mixed sand-coral substrata (Table 4.13). Differences in median length and length-group concentrations observed between homogeneous coral and rock-rubble bottom covers occur across the entire transition. Mixed rock-rubble substrata have significantly lower median species lengths with larger concentrations of species in the smallest length group (1-9.9 cm) at all points along the transition except one (Table 4.11). Bounding cumulative frequency curves constructed from all mixed bottom-cover categories show that size structure varies little within sand-coral and sand-rock-rubble substrata across the transition (Figure 4.8D). However, each occupies mutually exclusive zones reflecting significant differences in the size structure of their species assemblages.

While chi-square tests show no significant differences in proportions of species by length grouping for mixed bottom covers, there are significant increases in the median weight of species across this transition. Median species weights for mixed sand-coral substrata increase from 23 to 34 grams while mixed sand-rock-rubble substrata increase from 6 to 11 grams (Table 4.13, Figure 4.8A). In sand-coral mixtures, this change is due to increases in the number of species in both the 10-to-100 and 100-to-1000 gram weight classes, while in sand-rock-rubble mixtures only the 10-to-100 gram weight class increases (Table 4.13). Median weight increases across this gradient are significant for sand-coral mixtures, as demonstrated by one-way ANOVA results (Table 4.12). However, similar tests for sand-rock/rubble mixtures show no significant differences.

Table 4.13. Species characteristics and statistical tests for mixed sand-coral and sand-rock/rubble bottom covers. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	5-29%	30-49%	50-69%	70-89%	90-99%	100%
Mean Species Per Sample - Coral	13.6	17.9	19.9	21.2	18.8	20.9
Less than 10 grams	4	7	7.4	7.8	7.4	6.1
10 to 100 grams	6.1	6.5	7.7	8.5	8.3	8.9
100 to 1000 grams	2.9	3.6	4.2	4.2	4.4	5.2
1000-plus grams	0.6	0.7	0.6	0.6	0.6	0.5
Median Weight (grams) - Coral	22.8	23	28.9	24.9	25.8	34
Proportion Species by Weight Group						
Less than 10 grams	0.295	0.39	0.371	0.37	0.359	0.296
10 to 100 grams	0.451	0.366	0.387	0.403	0.4	0.428
100 to 1000 grams	0.213	0.204	0.211	0.201	0.214	0.252
1000-plus grams	0.041	0.041	0.031	0.027	0.027	0.025
Mean Species Per Sample - Rock/Rubble	13.3	21	18.9	19.5	21	19.6
Less than 10 grams	7.4	10.3	8.4	10.2	10.1	9.4
10 to 100 grams	2.5	6.3	6.8	5.4	7	6.4
100 to 1000 grams	2.8	4	3.1	3.6	3.4	3.2
1000-plus grams	0.6	0.3	0.6	0.4	0.5	0.6
Median Weight (grams) - Rock/Rubble	6	13.8	15.6	8.4	10.9	11.2
Proportion Species by Weight Group						
Less than 10 grams	0.557	0.492	0.444	0.521	0.481	0.479
10 to 100 grams	0.189	0.302	0.358	0.277	0.334	0.327
100 to 1000 grams	0.208	0.19	0.166	0.182	0.162	0.163
1000-plus grams	0.047	0.016	0.033	0.021	0.023	0.032
Chi-square Tests: Proportion Coral Species by Weight Group	5-29%	30-49%	50-69%	70-89%	90-99%	100%
5-29%		NS	NS	NS	NS	NS
30-49%	NS		NS	NS	NS	NS
50-69%	NS	NS		NS	NS	NS
70-89%	NS	NS	NS		NS	NS
90-99%	NS	NS	NS	NS		NS
100%	NS	NS	NS	NS	NS	
Chi-square Tests: Proportion Rock/Rubble Species by Weight Group	5-29%	30-49%	50-69%	70-89%	90-99%	100%
5-29%		NS	0.04	NS	0.08	0.09
30-49%	NS		NS	NS	NS	NS
50-69%	0.04	NS		NS	NS	NS
70-89%	NS	NS	NS		NS	NS
90-99%	0.08	NS	NS	NS		NS
100%	0.09	NS	NS	NS	NS	
Chi-square Tests: Proportion Rock/Rubble Species by Weight Group	5-29%	30-49%	50-69%	70-89%	90-99%	100%
Coral vs. Rock/Rubble	0.01	NS	NS	0.09	0.2	0.03

Abundance Characteristics and Comparisons for Homogeneous Substrate Types

Intersubstrate comparisons of mean and median abundance per sample are very similar to those observed for species. Complex substrata contain over 50 times the median number of fishes per sample as do sand bottom covers (Table 4.14). Between these extremes are the same two steps noted for species (Figure 4.11B). Mean abundance declines slowly from rubble to coral to rock substrata and then precipitously to grass bottom covers which contain three times the mean number of fishes found in sand substrata. However, median abundance is higher in rubble and rock substrata than in coral where the median is 73 percent of the mean (Figure 4.11A). Random samples of ten sites each also show lower mean abundance values in coral bottom covers. These differences result from a very small number of observations containing very large schools of small fishes which skew the mean for all sample sites. With one exception, one-way ANOVAs indicate no significant statistical differences between coral, rubble and rock pairings when computed for all sites and ten random samples of ten sites each (Table 4.15). The coral-rock pairing for the later case is significant at the 0.06 level. Other pairings between the complex substrata and grass or sand are significant at or above the 0.03 level.

Similarity indexes constructed from abundance by species show the same general characteristics as number of occurrences by species. Within-class index values are typically much larger than between-class values, although at slightly lower levels than species-occurrence indexes (Table 4.16, Figure 4.11D). Between-class values show the same three-stepped decline across the complexity gradient with a very large absolute gap in values between the more-complex substrata (coral, rock and rubble) and those of lower structural complexity (grass and sand).

Abundance Size Structure

The abundance of fishes for the five homogeneous bottom-cover classes show the same size shift that occurs in species. There is an increasing concentration of abundance in the smallest length and weight groups and a coincident decline in the numbers of larger fishes across the coral-to-sand complexity gradient (Table 4.14, Figure 4.11B). While one-way ANOVA's computed on mean abundance suggest few significant differences between coral, rock and rubble substrata, statistical tests focusing on size structure yield dramatic differences (Table 4.15).

The shift from coral to rock and rubble, while not significantly different in terms of total mean abundance, is significantly different when viewed from the perspective of size structure. There is a very large proportional decline in larger fishes, particularly in the 10-19.9 cm size group (Figure 4.11C), where absolute abundance is only 37 percent that of coral (Table 4.14). A similar decrease occurs in the 10-1000 gram weight group where abundance concentrations decline from 44 percent in corals to 23 and 18 percent respectively in rock and rubble (Table 4.14). This shift in cumulative frequency curves by length and weight (Figures 4.9 and 4.10) are confirmed by K-S statistics that suggest significant statistical differences between coral, rock and rubble substrata (Table 4.15). Chi-square tests conducted on abundance percentages by length group indicate statistical independence for all sample pairings except rock-rubble (Table 4.15).

Table 4.14. Abundance characteristics for homogeneous bottom-cover types.

	All Coral	All Rock	All Rubble	All Grass	All Sand
Sample Size	135	31	41	41	21
Mean Abundance Per Sample	304.8	260.5	326.2	45.8	14.8
1-9.9 cm	185.3	213	280.4	33.4	14.0
10-19.9 cm	92.4	31.2	35.8	2.4	0.7
20+ cm	27.2	16.4	9.9	10.0	0.2
Median Abundance Per Sample	222	239	271.5	34	4
Proportion Mean Abundance by Length Group					
All Lengths	1	1	1	1	1
1-9.9 cm	0.608	0.818	0.86	0.728	0.942
10-19.9 cm	0.303	0.12	0.11	0.053	0.045
20+ cm	0.089	0.063	0.03	0.219	0.013
Mean Abundance Per Sample (10 Random Samples of 10 Sites)	243.1	282.3	276.7	46.2	12.4
Mean Abundance Per Sample by Fish Weight					
Less than 1 gram	69.9	30.3	126.4	16.2	3.4
1 to 10 gram	99.4	169.8	139.9	20.4	10.4
10 to 100 grams	90.2	39.4	44.3	6.8	0.4
100 to 1000 gram	44.5	20	14.1	2	0.5
1000 plus gram	0.9	1.1	1.6	0.3	0.1
Proportion Abundance by Fish Weight					
Less than 1 gram	0.229	0.116	0.387	0.354	0.228
1 to 10 gram	0.326	0.652	0.429	0.446	0.704
10 to 100 grams	0.296	0.151	0.136	0.149	0.029
100 to 1000 gram	0.146	0.077	0.043	0.044	0.032
1000 plus gram	0.003	0.004	0.005	0.007	0.006

Table 4.15. Significance levels of statistical tests of abundance for homogeneous bottom-cover types. Numbers represent significant alpha levels below 0.20. NS equals 'not significant'.

Chi-square Tests: Proportion Abundance by Length Group	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.01	0.01	0.01	0.01
All Rock	0.01		NS	0.01	0.03
All Rubble	0.01	NS		0.01	0.16
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.03	0.16	0.01	
K-S Tests: Cumulative Frequency of Abundance by Fish Length	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.09	0.01	0.18	0.01
All Rock	0.09		0.06	NS	NS
All Rubble	0.01	0.06		0.02	0.02
All Grass	0.18	NS	0.02		0.03
All Sand	0.01	NS	0.02	0.03	
K-S Tests: Cumulative Frequency of Abundance by Fish Weight	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.07	0.01	0.01	0.01
All Rock	0.07		0.05	0.01	0.07
All Rubble	0.01	0.05		NS	0.01
All Grass	0.01	0.01	NS		0.04
All Sand	0.01	0.07	0.01	0.04	
One-Way ANOVA Tests: Mean Abundance Per Sample (All Sites)	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		NS	NS	0.01	0.01
All Rock	NS		NS	0.01	0.01
All Rubble	NS	NS		0.01	0.01
All Grass	0.01	0.01	0.01		0.03
All Sand	0.01	0.01	0.01	0.03	
One-Way ANOVA Tests: Mean Abundance Per Sample (10 Random Samples of 10 Sites)	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.06	NS	0.01	0.01
All Rock	0.06		NS	0.01	0.01
All Rubble	NS	NS		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	

Table 4.16. Abundance similarity indexes for homogeneous bottom-cover types constructed from 10 random samples of 10 sites each (Part A) and 1 site each (Part B). Proportion shared species are computed by dividing cell-specific shared species by total species for each row. Similarity indexes are computed from a modified version of Schoener's Index of Niche Overlap published by Gladfelter et al. (1980).

Part A: 10 Random Samples of 10 Sites Each.	All Coral	All Rock	All Rubble	All Grass	All Sand
Mean Abundance Per Sample	255.5	251.7	271.9	37.8	14.0
Modified Schoener's Index of Niche Overlap					
All Coral	0.834	0.557	0.565	0.083	0.007
All Rock	0.557	0.868	0.709	0.1	0.012
All Rubble	0.565	0.709	0.89	0.16	0.014
All Grass	0.083	0.1	0.16	0.79	0.095
All Sand	0.007	0.012	0.014	0.095	0.888
Part B: 10 Random Samples of 1 Site Each.	All Coral	All Rock	All Rubble	All Grass	All Sand
Mean Abundance Per Sample	271.1	262.3	257.6	39.8	15.6
Modified Schoener's Index of Niche Overlap					
All Coral	0.58	0.529	0.451	0.059	0.001
All Rock	0.529	0.674	0.585	0.088	0.009
All Rubble	0.451	0.585	0.774	0.108	0.01
All Grass	0.059	0.088	0.108	0.525	0.069
All Sand	0.001	0.009	0.01	0.069	0.748

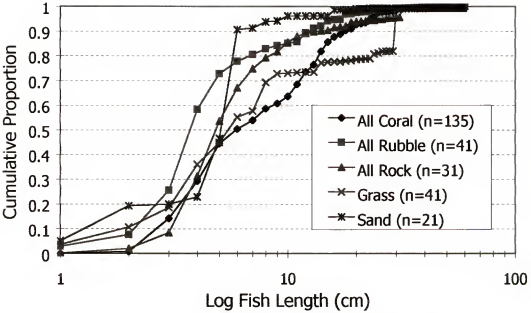

Figure 4.9. Cumulative frequency of abundance by fish length for homogeneous bottom-cover types.

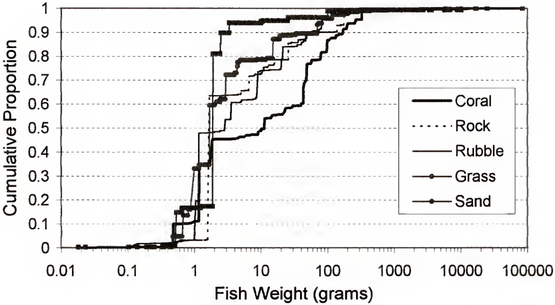

Figure 4.10. Cumulative frequency of abundance by fish weight for homogeneous bottom-cover types.

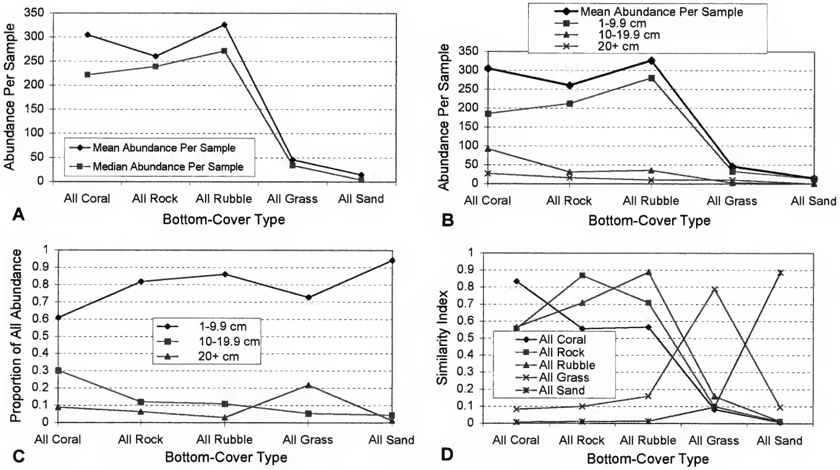

Figure 4.11. Abundance characteristics and similarity indexes for homogeneous bottom-cover types. A) Mean and median abundance. B) Mean abundance per sample: total and by length grouping. C) Abundance proportions by length grouping. D) Similarity indexes within and between homogeneous bottom-cover types.

As with species, there is a very large absolute decline in abundance across all length groups in the transition from the more complex substrata to grass and sand. Mean abundance in the 10-19.9 cm length group in coral substrata is 150 times greater than in sand. Grass bottom covers show a large proportional increase in the largest length group (20-plus cm) due to the occurrence of one large, transient planktivore (Inermia vittat) in several samples (Figure 4.11C). The exclusion of this species from the weight statistics explains the difference between the cumulative frequency curves of abundance by length and by weight (Figures 4.9 and 4.10).

Transitions in Abundance from Sand to Complex Substrate Types

Analysis of mixed bottom covers indicates that mean abundance per sample increases directly with the proportion of complex bottom cover, i.e., surface area. This relationship is more linear than that observed for species. However, like species, there are no obvious differences noted between the slopes of the three transition relationships (Figure 4.12C). One-way ANOVAs show significant differences between mean abundance for sand-coral and sand-rock/rubble mixtures at only one point across the surface-area gradient (Table 4.18). Simple linear regressions computed for mean abundance per sample and proportion complex substrate type in 10-percent bottom-cover increments resulted in R-square values of 0.82, 0.59 and 0.68 respectively. However, site-specific regressions of the same variables produced coefficient values of less than 0.09 in all instances. As noted for homogeneous sample sites, mixed sand-rubble substrata have consistently higher mean abundance than sand-coral and sand-rock mixtures (Figure 4.12C).

While there is much greater variation in site-specific abundance than for species (Figures 4.13A and C), one-way ANOVA results suggest that these increases across the surface-area gradient are significant for sand-coral mixtures (Table 4.18). These observations are reinforced by results obtained for 100 random samples of ten sites each drawn for eight sand-coral mixture classes. As shown in Figure 4.13B, quartile values from these samples show consistent increases across the surface-area gradient. As with species, statistical differences across the sand-rock/rubble transition are not as clear. While there appears to be a distinct, positive trend in mean and median values across the gradient (Figures 4.12C and 4.13C), one-way ANOVAs show consistent statistical differences only for pairings with the smallest proportional class (Table 4.18). This is perhaps a result of the very small sample sizes available for the intermediate sand-rock/rubble mixture classes.

While changes in total abundance across the transition are very similar between complex substrate types, size-specific structure and changes are very different. Chi-square tests indicate that size structure in sand-coral mixtures is significantly different from sand-rock/rubble mixtures at all points across the transition except one (Table 4.17). In sand-coral mixtures, abundance for all length and weight groupings increase from low to high coral cover at approximately the same rates and in the same general proportions (Figure 4.12A, B and D). Mixed sand-coral sample sites having a low proportion of coral initially display a greater concentration of abundance in the middle length group due to a couple of extreme observations and perhaps the smaller sample size. Beyond 29 percent coral cover, chi-square tests indicate no significant differences in size structure between homogeneous coral and mixed sand-coral substrata (Table 4.17). In sand-rock/rubble mixtures, larger fishes increase at much lower rates than smaller fishes resulting in a proportional shift in abundance to smaller sizes across the transition (Figure 4.12A). Here, chi-square tests indicate statistical independence in practically all pairings (Table 4.17).

Table 4.17. Abundance characteristics and statistical tests for mixed sand-coral and sand-rock/rubble bottom covers. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	5-29%	30-49%	50-69%	70-89%	90-99%	100%
Sample Size - Coral	9	37	146	178	105	135
Mean Abundance Per Sample - Coral	174.3	145.9	172.2	199.3	195.3	304.8
Less than 10 grams	33.6	78.5	101.8	103.7	99.5	169.3
10 to 100 grams	77.1	53.7	52.8	72.9	74.2	90.2
100 to 1000 grams	63	10.2	16.2	21.7	20.3	44.5
1000-plus grams	0.7	3.5	1.4	1	1.3	0.9
Proportion Abundance by Weight Group						
Less than 10 grams	0.192	0.538	0.591	0.52	0.51	0.555
10 to 100 grams	0.442	0.368	0.307	0.366	0.38	0.296
100 to 1000 grams	0.361	0.07	0.094	0.109	0.104	0.146
1000-plus grams	0.004	0.024	0.008	0.005	0.007	0.003
Sample Size - Rock/Rubble	6	5	8	20	33	63
Mean Abundance Per Sample -Rock/Rubble	82.1	202.7	267.1	207.2	303.5	278.4
Less than 10 grams	45.6	152.7	170	116.7	238.8	221.4
10 to 100 grams	11.6	23	74.5	40.6	36.6	41.8
100 to 1000 grams	22.9	26.7	22	49.4	26.5	14.1
1000-plus grams	2	0.3	0.6	0.6	1.5	1.1
Proportion Abundance by Weight Group						
Less than 10 grams	0.556	0.753	0.636	0.563	0.787	0.795
10 to 100 grams	0.142	0.113	0.279	0.196	0.121	0.15
100 to 1000 grams	0.279	0.132	0.082	0.238	0.087	0.051
1000-plus grams	0.024	0.002	0.002	0.003	0.005	0.004
Chi-square Tests: Proportion Coral Abundance by Weight Group	5-29%	30-49%	50-69%	70-89%	90-99%	100%
5-29%		0.01	0.01	0.01	0.01	0.01
30-49%	0.01		NS	NS	NS	0.18
50-69%	0.01	NS		NS	NS	NS
70-89%	0.01	NS	NS		NS	NS
90-99%	0.01	NS	NS	NS		NS
100%	0.01	0.18	NS	NS	NS	
Chi-square Tests: Proportion Rock/Rubble Abundance by Weight Group	5-29%	30-49%	50-69%	70-89%	90-99%	100%
5-29%		0.02	0.01	NS	0.01	0.01
30-49%	0.02		0.02	0.02	NS	0.13
50-69%	0.01	0.02		0.01	0.02	0.05
70-89%	NS	0.02	0.01		0.01	0.01
90-99%	0.01	NS	0.02	0.01		NS
100%	0.01	0.13	0.05	0.01	NS	
Chi-square Tests: Proportion Abundance by Weight Group	5-29%	30-49%	50-69%	70-89%	90-99%	100%
Coral vs. Rock/Rubble	0.01	0.01	NS	0.01	0.01	0.01

Table 4.18. Significance levels of statistical tests of abundance characteristics across the transition from sand to coral and sand to rock/rubble environments. Column headers refer to the percentage of coral or rock/rubble in the sand-coral or sand-rock/rubble mixture. Statistical test values represent significant alpha levels below 0.20. NS equals 'not significant'.

One-Way ANOVA Tests: Mean Abundance Per Sample (Sand-Coral Mixtures)	5 to 29%	30 to 39%	40 to 49%	50 to 59%	60 to 69%	70 to 79%	80 to 89%	90 to 99%	100%
5 to 29%		NS	NS	NS	NS	NS	NS	NS	0.1
30 to 39%	NS		NS	NS	0.04	0.12	0.01	0.02	0.01
40 to 49%	NS	NS		NS	NS	NS	0.04	0.15	0.01
50 to 59%	NS	NS	NS		0.01	0.11	0.01	0.01	0.01
60 to 69%	NS	0.04	NS	0.01		NS	0.2	NS	0.01
70 to 79%	NS	0.12	NS	0.11	NS		0.01	0.12	0.01
80 to 89%	NS	0.01	0.04	0.01	0.2	0.01		0.18	0.08
90 to 99%	NS	0.02	0.15	0.01	NS	0.12	0.18		0.01
100%	0.1	0.01	0.01	0.01	0.01	0.01	0.08	0.01	
One-Way ANOVA Tests: Mean Abundance Per Sample (Sand-Rock/Rubble Mixtures)	5 to 29%	30 to 49%	50 to 69%	70 to 89%	90 to 99%	100%			
5 to 29%		0.11	0.03	0.01	0.01	0.01			
30 to 49%	0.11		NS	NS	NS	NS			
50 to 69%	0.03	NS		NS	NS	NS			
70 to 89%	0.01	NS	NS		0.04	0.07			
90 to 99%	0.01	NS	NS	0.04		NS			
100%	0.01	NS	NS	0.07	NS				
Sand-Coral vs. Sand-Rock/Rubble	NS	NS	NS	NS	0.01	NS			

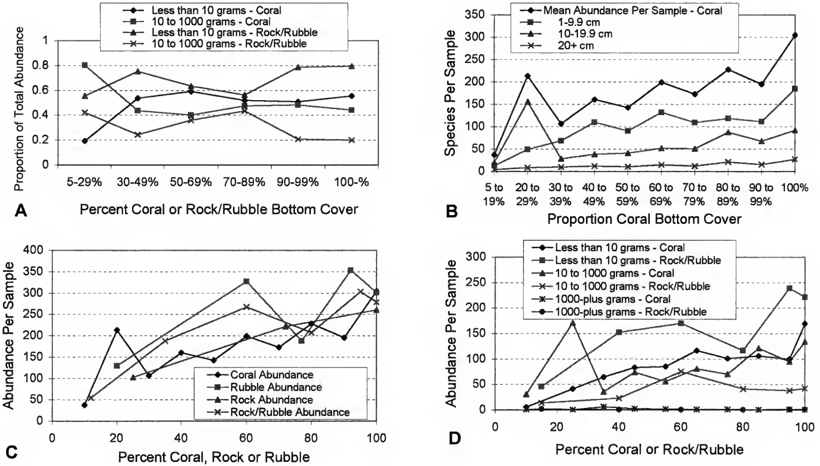

Figure 4.12. Abundance characteristics and comparisons across the sand-coral and sand-rock/rubble transition.
A) Mean and median abundance. B) Mean abundance per sample for sand-coral substrata: total and by length grouping.
C) Mean abundance per sample for sand-coral, sand-rock, sand-rubble and sand-rock/rubble mixtures.
D) Mean abundance per sample by weight group for sand-coral and sand-rock/rubble mixtures.

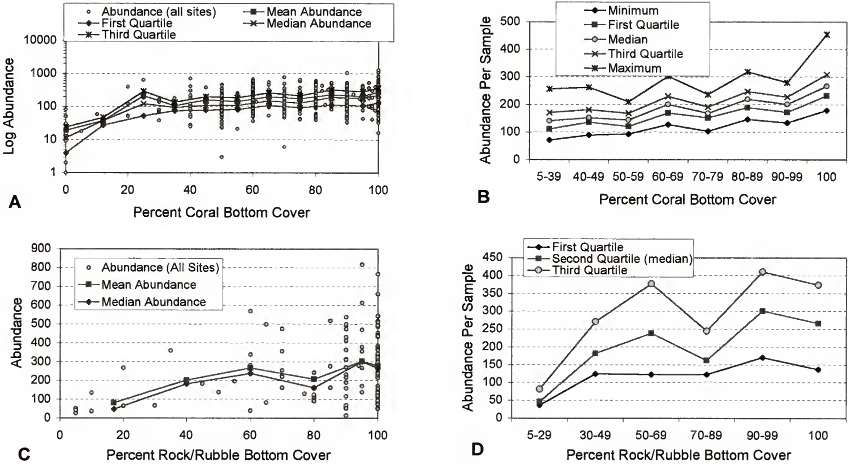

Figure 4.13. Statistical characteristics and comparisons of abundance across the sand-coral and sand-rock/rubble transition.

A) Site-specific abundance, quartiles and mean abundance across the sand-coral transition.

B) Abundance quartiles for 100 random samples of 10 sites each.

C) Site-specific abundance, mean abundance and median abundance across the sand-rock/rubble transition.

D) Abundance quartiles across the sand-rock/rubble transition.

Biomass Characteristics and Comparisons for Homogeneous Substrate Types

Total biomass at any sample site is computed as the sum of the products of species weights and abundance. While Bohnsack (1985) states that data collected using the stationary sampling technique should not be used for absolute density calculations, it must be pointed out that extrapolations of mean biomass per hectare for the complex bottom covers (Table 4.19) are well within the range of reef-fish standing-crop estimates (350 to 1950 kg ha^{-1}) produced independently by other authors (Goldman and Talbot, 1976; Mansaveta et al., 1986). Mean coral biomass lies at the center of this range, while mean rock and rubble biomass lie near the bottom (Table 4.19). Grass and sand biomass are much lower than the low end of these estimates.

Unlike abundance, which is skewed towards smaller fishes, biomass is concentrated in larger fishes. Mean and median biomass per sample displays the same overall decline across the complexity gradient as abundance and species. Coral substrata contain nearly 200 times the median biomass per sample as sand bottom covers. However, unlike abundance and species, there is a large, statistically significant break between coral and rock-rubble substrata. While these three bottom covers are very similar in terms of total species and abundance, mean and median coral biomass is nearly twice as large as rock or rubble (Table 4.19, Figure 4.16A). This, of course, is the result of size-structure differences, as biomass is computed as the product of weight and abundance. One-way ANOVAs computed across all samples for biomass confirm these differences (Table 4.19). Biomass changes between bottom-cover types also occur in two significant steps, only here, the non-significant pairings are rock-rubble and grass-sand. Coral substrata are significantly different at or above the 0.09 level in all pairings.

Table 4.19. Characteristics and statistical tests of biomass for homogeneous bottom-cover types. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'. Mean biomass per hectare is computed as 59.453 times mean biomass per sample. There are 59.453 sample areas per hectare (10000 m^2 / 168.2 m^2).

	All Coral	All Rock	All Rubble	All Grass	All Sand
Mean Biomass (grams) Per Sample	16784.8	8970	10080.5	3164.1	1712.2
1-9.9 cm	617.6	607.4	483.1	120.7	27.5
10-19.9 cm	5682.1	1628.2	2264	163	44.5
20+ cm	10485.1	6734.3	7333.5	2880.3	1640.2
Proportion Mean Biomass by Length					
All Lengths	1	1	1	1	1
1-9.9 cm	0.037	0.068	0.048	0.038	0.016
10-19.9 cm	0.339	0.182	0.225	0.052	0.026
20+ cm	0.625	0.751	0.727	0.91	0.958
Median Biomass (grams) Per Sample	8870	4530	5480	151	41
Mean Biomass (kg) Per Hectare	997.9	533.3	599.4	188.1	101.8
Proportion Biomass by Fish Weight					
Less than 1 gram	0.002	0.002	0.006	0.002	0.001
1 to 10 gram	0.016	0.046	0.033	0.016	0.014
10 to 100 grams	0.234	0.132	0.163	0.068	0.004
100 to 1000 gram	0.57	0.466	0.377	0.168	0.035
1000 plus gram	0.178	0.354	0.42	0.746	0.945
Chi-square Tests: Proportion Biomass by Length Group	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.03	0.2	0.01	0.01
All Rock	0.03		NS	0.01	0.01
All Rubble	0.2	NS		0.01	0.01
All Grass	0.01	0.01	0.01		NS
All Sand	0.01	0.01	0.01	NS	
K-S Tests: Cumulative Frequency of Biomass by Fish Length	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.01	0.01	0.01	0.01
All Rock	0.01		NS	0.01	0.01
All Rubble	0.01	NS		0.01	0.01
All Grass	0.01	0.01	0.01		NS
All Sand	0.01	0.01	0.01	NS	
One-Way ANOVA Tests: Mean Biomass Per Sample	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		0.09	0.05	0.01	0.02
All Rock	0.09		NS	0.01	0.06
All Rubble	0.05	NS		0.01	0.04
All Grass	0.01	0.01	0.01		NS
All Sand	0.02	0.06	0.04	NS	

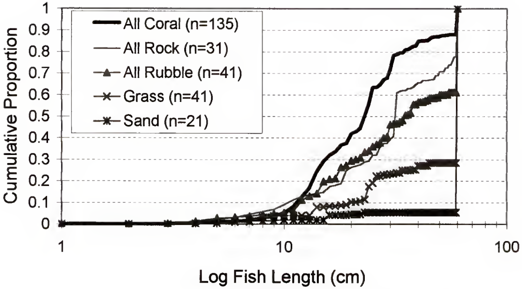

Figure 4.14. Cumulative frequency of biomass by fish length for homogeneous bottom-cover types.

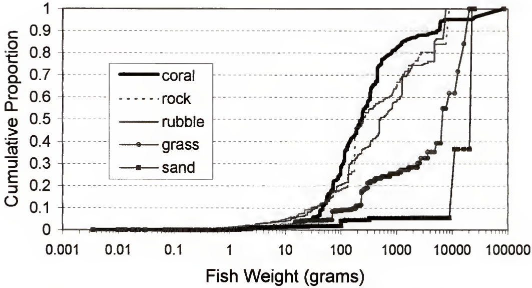

Figure 4.15. Cumulative frequency of biomass by fish weight for homogeneous bottom-cover types.

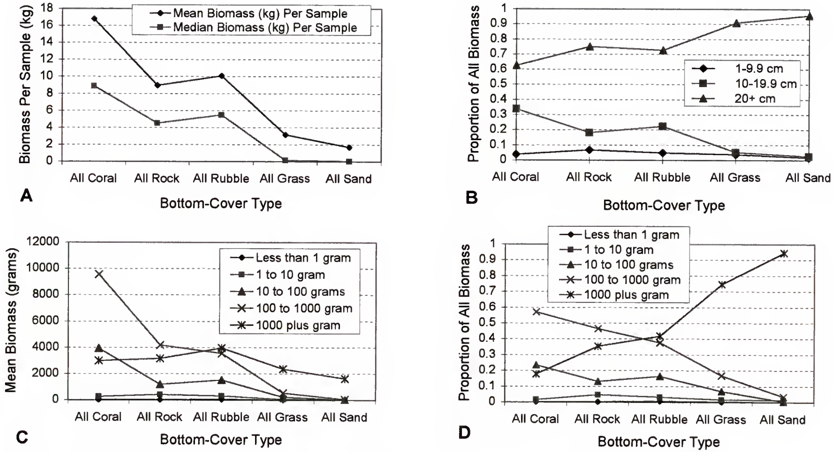

Figure 4.16. Biomass characteristics and comparisons for homogeneous bottom-cover types. A) Mean and median biomass per sample. B) Biomass proportions by length grouping. C) Mean biomass per sample by weight grouping. D) Biomass proportions by weight grouping.

Grass-sand differences, which were significant in species and abundance, are not significant in respect to biomass, even though grass bottom covers contain nearly twice the mean biomass of sand.

The distribution of biomass across the five homogeneous bottom-cover types is a mirror image of the size shift that occurs in species and abundance. While total biomass declines in all length groupings across the gradient, it declines least in the largest fishes (Table 4.19). When viewed by weight, fishes greater than 1000 grams show very little change across the gradient, while fishes in the 10-to-1000 gram weight classes decline dramatically (Figure 4.16C). This results in an almost linear shift in biomass proportions to the largest weight class (Figure 4.16D). Instead of shifting to the left, the cumulative frequency curves shift to the right (Figures 4.14 and 4.15) as the medium-sized fish groups, which are so well developed in coral bottom covers, quickly disappear across the complexity gradient (Figures 4.16B, C and D). These changes in the medium-sized fish groups explain the differences in biomass structure between coral, rock and rubble substrata.

Statistical tests confirm two significant breaks in size structure between the five homogeneous substrate types. Chi-square tests conducted on biomass percentages by length and weight groups (Table 4.19) indicate statistical independence for all sample pairings except rock-rubble and grass-sand. K-S statistics (Table 4.19) show the same results.

Fish Characteristics and Comparisons for Forereef and Backreef Environments

In typical coral-reef systems the scale of forereef structures are frequently very different from those found in lower-energy backreef environments. Both vertical relief and horizontal extent are typically greater in the forereef environment, which corresponds to the zone of most prolific coral growth. Similarly, the range of object sizes, either as growth forms in corals or bio-clastic sediments in rubble, may decline in lower-energy environments. Related variables such as surface area and surface geometry should correspondingly vary between these two zones. If substrate geometry influences fish size and mass distributions, then intersubstrate relationships within backreef environments should be similar to those in forereef environments, only at scales commensurate with the magnitude of the structures involved.

Species, Abundance and Biomass Characteristics

Analysis of forereef and backreef sample sites indicate that intersubstrate relationships are very similar to aggregate samples and of magnitudes that would seem to reflect the expected changes in geometry between these two environments. In general, species, abundance and biomass decrease significantly from forereef to backreef but intersubstrate relationships are similar within each zone. The mean number of species per sample are 26, 12 and 20 percent lower respectively for coral, rock and rubble substrata in the backreef environment (Table 4.20). One-way ANOVA's indicate that these differences, with the exception of forereef rock, are significant between zones but not within (Table 4.20). Like species, abundance is significantly lower in backreef locations: 34 and 54 percent of mean forereef coral and rubble values respectively (Table 4.21). Like aggregate samples, median abundance increases from coral to rubble in each zone. While biomass is significantly greater in forereef zones, relationships between substrata within zones show the same significant differences as aggregate samples. Forereef corals contain nearly two and three times the biomass of forereef rubble and forereef rock respectively. However, median backreef coral biomass is not significantly different from backreef rubble (Table 4.22). This is due, in part, to a seemingly abnormal

Table 4.20. Species characteristics and statistical tests for homogeneous bottom-cover types by forereef and backreef location. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rock	Backreef Rubble
Sample Size	96	21	38	36	7	24
Mean Species Per Sample	22.4	19.4	22.6	16.6	17	18.2
1-9.9 cm	8.3	10.2	12.4	7.7	10.3	13
10-19.9 cm	8.8	6	6.1	5.8	4.6	3.4
20+ cm	5.2	3.2	4.1	3.1	2.1	1.8
Mean Fish Length (cm)	14.4	12.5	12.3	12.5	11.5	9.7
Median Fish Length (cm)	11.5	8.5	8	9.4	7.4	6
Proportion Species by Length						
All Lengths	1	1	1	1	1	1
1-9.9 cm	0.373	0.525	0.548	0.463	0.605	0.716
10-19.9 cm	0.394	0.309	0.269	0.352	0.269	0.188
20+ cm	0.233	0.167	0.183	0.185	0.126	0.096
Median Fish Weight (grams)	40.5	14.6	15.5	22.2	10.3	3.1
Proportion Species by Weight						
Less than 10 grams	0.269	0.442	0.436	0.384	0.484	0.715
10 to 1000 grams	0.705	0.53	0.532	0.599	0.516	0.262
1000-plus grams	0.027	0.029	0.032	0.017	0	0.024
Chi-square Tests: Proportion Species by Length	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rock	Backreef Rubble
Forereef Coral		0.1	0.05	NS	0.01	0.01
Forereef Rock	0.1		NS	NS	NS	0.03
Forereef Rubble	0.05	NS		NS	NS	0.05
Backreef Coral	NS	NS	NS		0.13	0.01
Backreef Rock	0.01	NS	NS	0.13		NS
Backreef Rubble	0.01	0.03	0.05	0.01	NS	
One-Way ANOVA Tests: Mean Species Per Sample	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rock	Backreef Rubble
Forereef Coral		0.01	NS	0.01	0.01	0.01
Forereef Rock	0.01		0.01	0.07	NS	NS
Forereef Rubble	NS	0.01		0.01	0.01	0.01
Backreef Coral	0.01	0.07	0.01		NS	NS
Backreef Rock	0.01	NS	0.01	NS		NS
Backreef Rubble	0.01	NS	0.01	NS	NS	
One-Way ANOVA Tests: Median Weight Per Sample	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rock	Backreef Rubble
Forereef Coral		0.01	0.01	0.05	0.01	0.01
Forereef Rock	0.01		NS	0.04	NS	0.01
Forereef Rubble	0.01	NS		0.04	NS	0.01
Backreef Coral	0.05	0.04	0.04		0.18	0.01
Backreef Rock	0.01	NS	NS	0.18		0.09
Backreef Rubble	0.01	0.01	0.01	0.01	0.09	

Table 4.21. Abundance characteristics and statistical tests for homogeneous bottom-cover types by forereef and backreef location. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rubble
Sample Size	96	22	38	36	24
Mean Abundance Per Sample	373.3	314.9	371.6	128	199.6
1-9.9 cm	223.3	264.5	314.9	81.6	185.7
10-19.9 cm	115.6	29.8	44.6	36.8	10.7
20+ cm	34.4	20.6	12.1	9.6	3.3
Median Abundance Per Sample	298	313.5	330.5	97.5	128.5
Proportion Mean Abundance by Length Group					
1-9.9 cm	0.598	0.84	0.848	0.637	0.93
10-19.9 cm	0.31	0.095	0.12	0.288	0.053
20+ cm	0.092	0.065	0.033	0.075	0.016
Mean Abundance Per Sample (10 Random Samples of 10)	358.1	292.9	372.5	137.6	188.1
Mean Abundance by Fish Weight					
Less than 10 grams	204.8	250.2	269.6	71.9	170.1
10 to 1000 grams	167.3	63.6	71.3	55.8	28.9
1000-plus grams	1.1	1	1.6	0.3	0.6
Proportion Abundance by Weight					
Less than 10 grams	0.549	0.795	0.787	0.561	0.852
10 to 1000 grams	0.448	0.202	0.208	0.436	0.145
1000-plus grams	0.003	0.003	0.005	0.003	0.003
Chi-square Tests: Proportion Abundance by Length Group	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rubble
Forereef Coral		0.01	0.01	NS	0.01
Forereef Rock	0.01		NS	0.01	0.1
Forereef Rubble	0.01	NS		0.01	0.17
Backreef Coral	NS	0.01	0.01		0.01
Backreef Rubble	0.01	0.1	0.17	0.01	
K-S Tests: Cumulative Frequency of Abundance by Fish Length	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rubble
Forereef Coral		0.11	0.01	NS	0.01
Forereef Rock	0.11		0.05	0.08	NS
Forereef Rubble	0.01	0.05		0.01	NS
Backreef Coral	NS	0.08	0.01		0.01
Backreef Rubble	0.01	NS	NS	0.01	

Table 4.22. Biomass characteristics and statistical tests for homogeneous bottom-cover types by forereef and backreef location. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'. Mean biomass per hectare is computed as 59.453 times mean biomass per sample. There are 59.453 sample areas per hectare (10000 m^2 / 168.2 m^2).

	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rubble
Sample Size	96	21	38	36	24
Mean Biomass Per Sample (grams)	21248.9	8071.3	11353.9	5925	8064.4
1-9.9 cm	674.9	728	461.1	483.3	517.8
10-19.9 cm	7272.6	1251.3	3250.9	1841.4	701.3
20+ cm	13301.4	6092	7641.9	3600.3	6845.2
Median Biomass Per Sample (grams)	12120	4790	7310	3430	3380
Mean Biomass (kg) Per Hectare	1263.3	479.8	675.0	352.3	479.4
Proportion Mean Biomass by Length					
1-9.9 cm	0.032	0.09	0.041	0.082	0.064
10-19.9 cm	0.342	0.155	0.286	0.311	0.087
20+ cm	0.626	0.755	0.673	0.608	0.849
Mean Biomass Per Sample (10 Random Samples of 10 Sites Each)	20173	6695.8	10834.7	4102	7493.3
Mean Biomass by Weight (grams)					
Less than 10 grams	328.1	533.6	338	224.5	305.3
10 to 1000 grams	17160.7	5756.7	6784.6	4625.8	1615.1
1000-plus grams	3760.1	1781.1	4231.3	1074.6	6144
Proportion Biomass by Fish Weight					
Less than 10 grams	0.015	0.066	0.03	0.038	0.038
10 to 1000 grams	0.808	0.713	0.598	0.781	0.2
1000-plus grams	0.177	0.221	0.373	0.181	0.762
Chi-square Tests: Proportion Biomass by Length Group	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rubble
Forereef Coral		0.01	NS	NS	0.01
Forereef Rock	0.01		0.05	0.04	NS
Forereef Rubble	NS	0.05		NS	0.01
Backreef Coral	NS	0.04	NS		0.01
Backreef Rubble	0.01	NS	0.01	0.01	
K-S Tests: Cumulative Frequency of Biomass by Length	Forereef Coral	Forereef Rock	Forereef Rubble	Backreef Coral	Backreef Rubble
Forereef Coral		0.02	0.08	NS	0.01
Forereef Rock	0.02		NS	0.07	0.01
Forereef Rubble	0.08	NS		0.19	0.01
Backreef Coral	NS	0.07	0.19		0.01
Backreef Rubble	0.01	0.01	0.01	0.01	

concentration of very large barracudas (100-plus cm) in 2 of the 24 backreef rubble sample sites. Backreef coral biomass concentrated in the 1-19.9 cm length groups is two times that of backreef rubble.

Mean and median species lengths also decline from forereef to backreef environments, as do median species weights. All three display the same general magnitude of decline between coral, rock and rubble (Table 4.20, Figure 4.17C). Median species length and weight for backreef coral is, in fact, higher than for forereef rubble and rock. One-way ANOVAs suggest that species-weight differences are significant for all substrate pairings except for those involving forereef rock, forereef rubble and backreef rock (Table 4.20). The latter may be largely the result of sample size. Substrate-specific median length and weight differences between zones may result from smaller surface-area geometry attributable to lower relief or to differences in larger-scale surface morphology.

Size Structure in Species, Abundance and Biomass

Size-structure shifts of similar magnitudes occur in species, abundance and biomass between substrate types in both zones. There is a dramatic increase in the proportion of species and abundance concentrated in the smallest length and weight groups and a coincident decline in larger sizes as bottom covers change from coral to rubble in both zones (Figures 4.17B and D, Tables 4.20 and 4.21). Coral bottom covers contain a larger proportion of total species, abundance and biomass in the middle length and weight groups in both zones than do rock and rubble substrata (Tables 4.20, 4.21 and 4.22).

Despite differences in absolute species, abundance and biomass, fish size structures in coral bottom covers are statistically similar between zones. Backreef coral is the only bottom-cover

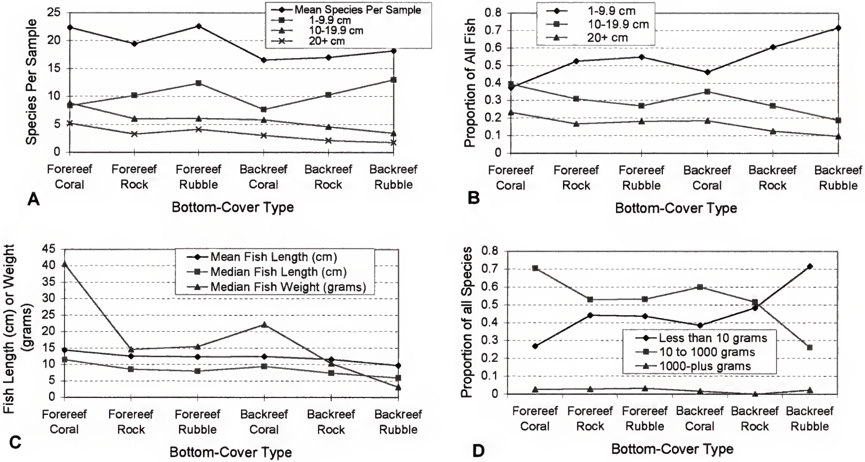

Figure 4.17. Species characteristics and comparisons for homogeneous bottom-cover types by forereef and backreef location. A) Mean species per sample: total and by length grouping. B) Species proportions by length grouping. C) Mean species length and median species length and weight. D) Species proportions by weight grouping.

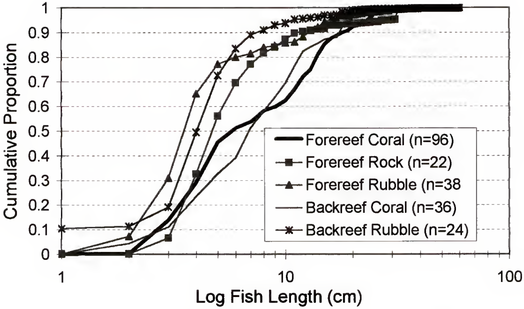

Figure 4.18. Cumulative frequency of abundance by fish length for homogeneous bottom-cover types by forereef and backreef location.

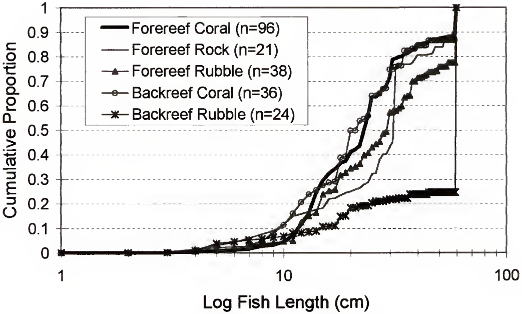

Figure 4.19. Cumulative frequency of biomass by fish length for homogeneous bottom-cover types by forereef and backreef location.

type whose proportional length and weight concentrations are not significantly different from forereef coral. Chi-square tests for species (Table 4.20) and abundance (Table 4.21) proportions by length group indicate that forereef coral is significantly different from all other bottom covers except backreef coral. Similar results are shown by K-S tests indicating that cumulative abundance and biomass curves for forereef and backreef corals are not significantly different (Figures 4.18 and 4.19). Backreef rock substrata sho2w significant statistical differences in species size proportions only in pairings with forereef and backreef coral substrata (Table 4.20). However, this sample size is very small. Unlike coral bottom covers, rubble substrata show significant interzonal differences in al size-structure indices (Tables 4.20, 4.21 and 4.22).

These results suggest that interzonal fish-population size structures are statistically similar for hard substrate types such as coral and rock, but significantly different for coarse detrital bottom covers. These differences may simply reflect the mechanical size grading which occurs in sediments between zones, whereas interzonal geometric differences between hard substrata are not as pronounced. Significant differences in the absolute numbers of species, abundance and biomass between zones, particularly for coral bottom covers, are not as easily explained. Such differences for homogeneous sites having the same two-dimensional surface area may result from lower overall surface area or smaller surface-area geometry due to lower vertical relief or differences in the mixture of coral genera or energy-related growth forms.

Comparisons of Homogeneous Substrate Size-Structure Ranges

Results from the preceding sections indicate that fish-population size structure is very different between the five substrate types. To further evaluate these differences, a series of upper and lower bounds were constructed for species and abundance in forereef and backreef environments for each substrate type based on 95-percent confidence intervals about the mean of one-centimeter length increments computed across cumulative frequency curves for all sample sites. In the case of grass and sand, where all samples were collected in the backreef environment, these bounds were constructed from the means for all sample sites.

These bounding cumulative frequency curves (Figure 4.20) indicate that the species size structures for each of the five substrate types occupy unique, limited size ranges which overlap at their extremes, but not over their entire range. In all cases, size curves for forereef structures define the upper bounds of the confidence interval and backreef structures define the lower bounds. Differences in the shape of these bounding size curves are primarily a function of species concentrations in the middle size ranges: the 10-19.9 cm length group. Coral substrata contain large concentrations of species in this size range. Consequently, the bounding size curves take on the shape of a more normal cumulative distribution. As species concentrations in the middle size ranges decline, the curves steepen in the smaller sizes and flatten in the middle, indicative of a positively skewed distribution. Sand and grass substrata which have the smallest median fish lengths (5.13 and 4.89 cm) and the largest concentration of species in the smallest length grouping (71.9 and 79.4 percent) occupy the extreme left of the size distributions, overlapping rubble distributions in their lower range. Rubble and coral distributions overlap slightly at their upper and lower bounds respectively. Bounding size curves for rock substrata lie between rubble and coral, overlapping rubble distributions in their upper ranges and coral distributions in their lower ranges.

Bounding cumulative frequency curves for abundance (Figure 4.21) have greater ranges than for species due to greater variances in abundance between individual sample sites. They

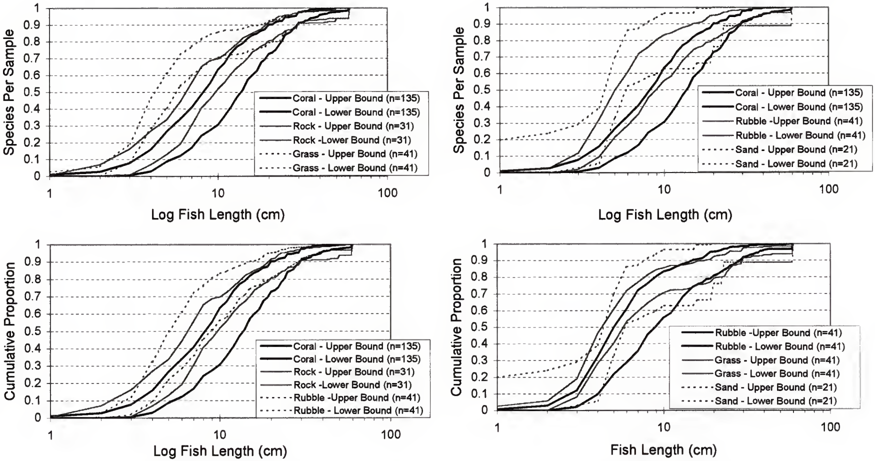

Figure 4.20. Species bounding cumulative frequency curves for homogeneous bottom-cover types. Upper and lower bounds were constructed for each bottom-cover type based on 95 percent confidence intervals about the mean of 1-centimeter length increments in the mean cumulative frequency curves for species in forereef and backreef locations. Bounds for grass and sand were constructed from means for all sample sites.

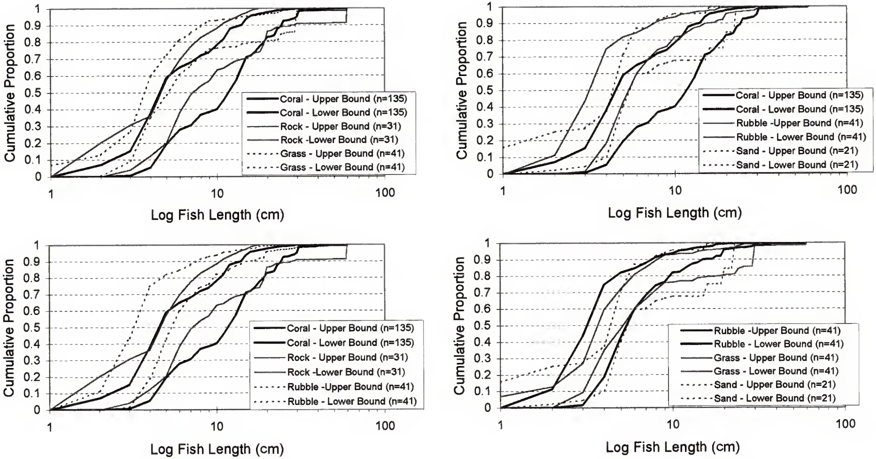

Figure 4.21. Abundance bounding cumulative frequency curves for homogeneous bottom-cover types. Upper and lower bounds were constructed for each bottom-cover type based on 95 percent confidence intervals about the mean of 1-centimeter length increments in the mean cumulative frequency cures for abundance in forereef and backreef locations. Bounds for grass and sand were constructed from the means for all sample sites.

are also skewed to smaller sizes, as abundance is greater in smaller fishes. However, they show the same general relationships between the five substrate types. Fish populations in forereef structures define the upper boundary of the confidence interval while those in backreef structures define the lower boundary. Sand, grass and rubble size ranges tend to overlap as their bounding size curves are compressed into very small fish sizes. Coral abundance size ranges expand but retain their relationship to rubble substrata, which marginally overlap their lower bounds. As in species distributions, rock cumulative size curves lie between coral and rubble distributions, overlapping their lower and upper bounds respectively.

Body-Mass Frequencies and Discontinuities in Fish Populations

The previous sections have shown that differences between homogeneous substrate types occur because of significant shifts in the concentration of species and abundance to smaller sizes. Do these shifts reflect changes in the dominant geometric substrate frequencies? If so, then comparisons of species density measures and body-mass concentrations may provide further information on the nature of these changes.

Frequencies and Discontinuities in Species Sizes: Gap Analysis

Holling (1992) suggests that the dominant frequencies of animal body mass in landscapes can be identified by locating the gaps in size-ordered species distributions that define their boundaries. The gaps represent size ranges in the distributions where the distances between elements are abnormally large in relation to the means for surrounding size ranges. The dominant frequencies are represented by those size ranges having very small differences (gaps) between species body sizes. To conduct this 'gap analysis', two additional data sets were constructed from size-ordered species weights for each of the homogeneous bottom covers. The first set consists of median weights for all observed species. The second set contains measurements of the second, third and fourth quartiles (25th, 50th and 75th percentiles) for each observed species, and are included in the analysis to more adequately represent the body sizes of species with multi-modal distributions. Only one observation was retained where species-specific quartile values were the same. Gap-index values were calculated for each data set by applying a split-moving-window ratio of summed sizes across the rank-ordered observations. This formula is expressed as $DI_n = 1 - ((S_n + S_{n-1}) / (S_n + S_{n+1}))$, where 'n' equals the rank-ordered observation and 'S' equals species weight in grams. A generalized set of index values was then created from a running average of seven values for each point in the rank-ordered distributions.

Analysis of the gap-index distributions reveals several general observations. First, the overall shapes of the curves reflect the macro-characteristics of species weight distributions across all fish-size observations. As expected, gaps are largest in the tails of the distributions where species observations are scarce and are lowest in those size ranges where most species are concentrated (Figure 4.22). Second, the absolute magnitude of the gaps in the macro-distributions is dependent on the number of observations. The gap-index values produced from median species weights are larger than those produced from quartile rankings (Figures 4.22A and B). These, in turn, are larger than those developed from observations that include species-specific sizes from all sample sites (Figure 4.22D). At this scale, all distributions appear to be uni-modal with the exception of grass bottom covers, where two distinct clusters are apparent (Figures 4.22B and C). Sand bottom covers display one cluster in the smallest size ranges, while all other species observations are widely scattered (Figure 4.22C).

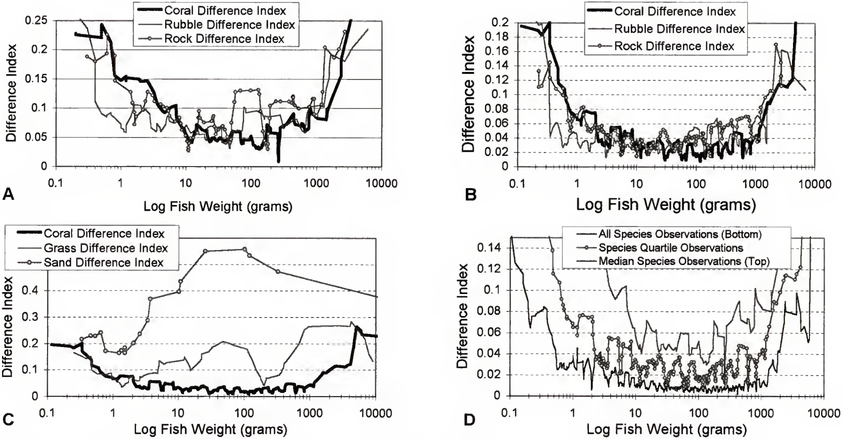

Figure 4.22. Difference (gap) indexes for homogeneous coral, rock, rubble, grass and sand bottom covers calculated from size-ordered species weights using the formula $DI = 1 - ((S_n + S_{n-1}) / (S_n + S_{n+1}))$, where 'n' equals the rank-ordered observation and 'S' equals species weight. Values shown in these graphs are running averages of 7 difference index values.

A) Fish-size difference indexes for coral, rock and rubble based on median species weights.

B) Fish-size difference indexes for coral, rock and rubble based on species-weight quartiles 1, 2 and 3.

C) Fish-size difference indexes for coral, grass and sand based on species-weight quartiles 1, 2 and 3.

D) Comparisons of difference indexes for coral based on 3 sets of species weight observations: medians, quartiles, all samples.

The macro-scale curves distinctly show the size shifts that occur in the transition between bottom-cover types. The low points are very close to the median species weight values observed earlier in this study (Figures 4.22B and C). The lower gap-index values for rock and rubble species observations of less than 10 grams occur because of the greater concentration of specie observations in this size range (Figure 4.22B). Similarly, the higher index values in the 60-to-1000 gram size range occur because of decreases in species observations in these sizes. Thus, the size shifts which occur from coral to non-coral bottom covers due to changes in size-specific specie occurrences, weights and numbers of fishes are manifested in increasing mid-range gap-index values and declining index values in the smallest size ranges.

Superimposed on these macro-scale curves are numerous smaller body-mass clusters that may or may not reflect size-specific breaks in the geometry of reefscapes. As the number of observations increase, the size of these larger-scale gaps decline (Figure 4.22). However, many continue to occur in the same general locations suggesting that they may be real phenomena and not the results of random factors or averaging techniques. Any further analysis of these large-scale clusters and gaps are beyond the scope of this research.

Frequencies and Discontinuities in Body Mass

Morse et al. (1985) demonstrated that the number of arthropods occupying fractal vegetation surfaces displayed an inverse power relationship to body size. This relationship forms a straight line when plotted as a log-log function. The Textural-Discontinuity Hypothesis suggests that changes in the slope of such power functions reflect changes in the geometric characteristics or architectural properties of landscapes which affect the entrained mass of animals by increasing or reducing the available resources or carrying capacity of landscapes at particular scales (Holling, 1992). This argument suggests that relationships between numerical fish properties (occurrences, abundance and body mass) and fish body sizes (length and weight) can be used to identify and compare dominant frequencies and discontinuities in fish-population size structure within and between bottom-cover types. To test this proposal, specie occurrences, abundance and body mass were summed by 1-cm length increments and 0.01 log weight increments for each of the homogeneous bottom-cover types and normalized for a sample size of 100 sites. A new set of trend-line estimates was then created for each numerical measure by applying a rolling regression technique to each point in the data series. Starting with the third and eleventh size-ordered observations respectively for the length and weight data sets, slope and y-intercept values were calculated for a linear regression line passing through two and ten data points respectively on either side of the starting position. In all cases, the independent variable is fish body length or weight and the dependent variable is occurrences, abundance, biolength or biomass. Biolength is an intermediate measure of body mass that is derived as the product of abundance and length. Dependent variable estimates were then calculated by substituting point-specific slope, y-intercept and independent variable values into the formula $y = ax + b$.

When plotted as log-log functions, the rolling-regression data sets indicate that fish species occurrences and abundance do display an inverse, linear relationship to fish body size over many areas of the length and weight size spectrums. However, there are major discontinuities in the slopes of these relationships, which occur at approximately the same sizes within all bottom-cover types. These breaking points appear to correspond with at least two dominant size frequencies which are clearly visible in the distributions of biolength and biomass (Figures 4.23 and 4.24). The negative slope of these relationships in the smallest fish sizes may reflect a

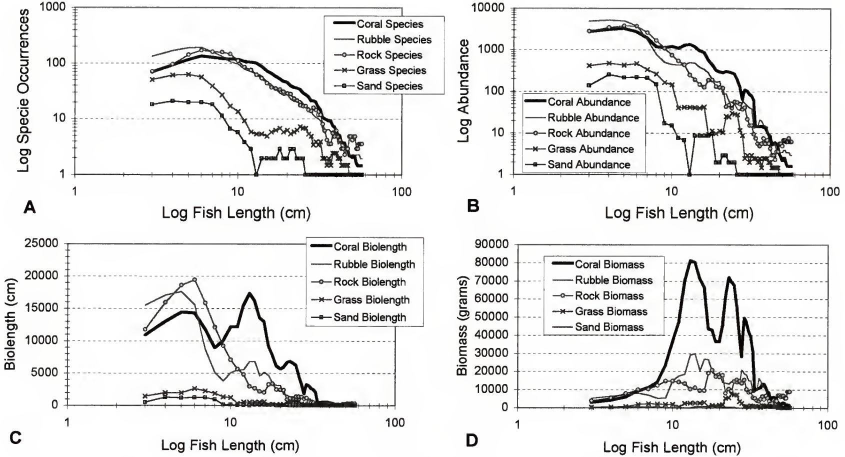

Figure 4.23. Rolling regression estimates of species, abundance, biolength and biomass by fish length for coral, rock, rubble, grass and sand bottom covers. Values were constructed in 1-cm length increments based on the formula y = ax + b, where a and b were obtained from a moving least-squares regression of 5 x and y values centered on the estimate point. Data were normalized as units per 100 samples. Biolength is an intermediate measure of fish mass computed as length times abundance.
A) Log-log plot of specie occurrences and fish length. B) Log-log plot of abundance and fish length.
C) Plot of biolength and log fish length. D) Plot of biomass and log fish length.

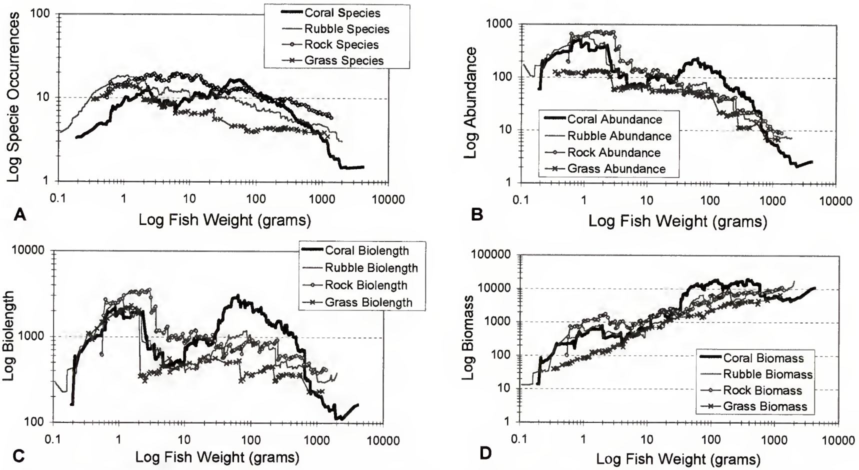

Figure 4.24. Rolling regression estimates of species, abundance, biolength and biomass by fish weight for coral, rock, rubble, and grass bottom covers. Values were constructed in log-weight increments based on the formula $y = ax + b$, where a and b were obtained from a moving least-squares regression of 21 x and y values centered on the estimate point. Data were normalized as units per 100 samples. Biolength is an intermediate measure of fish mass computed as length times abundance.
A) Log-log plot of specie occurrences and fish weight. B) Log-log plot of abundance and fish weight.
C) Log-log plot of biolength and fish weight. D) Log-log plot biomass and fish weight.

lower bound in fish body weights, or it may represent an observation threshold beyond which it is extremely difficult to accurately enumerate fish populations by visual methods.

When measured by length, the complex bottom covers display a convex occurrences-to-length relationship, which appears to be uni-modal as compared to the distinctly bi-modal distributions of grass and sand (Figure 4.23A). Inflection points on the species-occurrence curves of all bottom covers are located in the 5-7, 11-12 and 25-35 cm length ranges (Figure 4.23A) and correspond with major high points in the concentrations of fish abundance, biolength and biomass (Figures 4.23B, C and D).

When measured by weight, the size distributions become distinctly bi-modal. Coral bottom covers display two dominant frequencies, which are centered between 0.8 to 2 grams and 40 to 100 grams (Figures 4.24A, B, C and D). These frequencies appear to be shared between all bottom-cover types. Differences in the concentrations of species and abundance in each size range explain the differences between bottom-cover size structures. These results are consistent with those of previous sections.

The Effects of Seasonal Variations in Abundance

Bohnsack et al. (1992) noted that large seasonal fluctuations in abundance occur in many areas of the Florida Reef Tract. To test whether seasonal variations have any effect on fish-population size structure, samples sites for each of the three complex bottom-cover types (coral, rock and rubble) were coded by season (spring, summer, fall and winter) based on the dates that the samples were conducted. Only coral bottom covers had enough winter samples to compare with the other months. Grass and sand substrata could not be seasonally compared as practically all of these samples were collected in the summer months.

Analysis of the homogeneous sample sites indicates significant seasonal differences in mean abundance for coral, rock and rubble substrata. The mean number of fishes present in complex bottom covers are lowest in the winter or spring months and progressively increase with peak values occurring in the fall (Table 4.23). All three bottom covers have fall abundance values that are between 1.5 and 2.5 times higher than their winter or spring lows. All fish size groups increase across the seasonal transition. The number and proportion of small fishes (1-9.9 cm) rises rapidly in summer and levels off in the fall months. Medium and large fishes increase slowly through summer, then display a large increase in the fall. This cycle is consistent for all substrate types.

There are seasonal changes in median species lengths that accompany this lagged cycle between small and large fishes. Median lengths decline from winter or spring to summer where they reach a low point coincident with the small-fish peak. As larger fishes increase in the fall months, median species lengths increase (Table 4.23). Chi-square tests indicate that fish-population size structure in the summer months is significantly different at or above the 0.06 level from either spring or fall in all complex bottom covers. However, no season was statistically independent in pairings with the mean for all seasons.

The significant, intersubstrate size-structure differences observed between the aggregate, homogeneous bottom-cover samples occur at all points along the seasonal transition. Median species lengths in coral bottom covers are significantly higher in all seasons than those in rock and rubble substrata (Table 4.23). Similarly, chi-square tests conducted on percentage abundance distributions by length group show statistical independence at the 0.01 level for all seasonal pairings of coral with rock and rubble sample sites (Table 4.23). Conversely, similar statistical comparisons of rock and rubble samples show no significant differences in any

Table 4.23. Abundance characteristics by season for homogeneous bottom-cover types.

	Winter	Spring	Summer	Fall	All Samples
CORAL: Sample Size	16	37	69	10	135
Mean Abundance Per Sample	185.6	227.9	341.4	521.6	304.8
Median Fish Length (cm)	11.6	11.1	10.6	12.2	11
Proportion Abundance by Length Group					
1-9.9 cm	0.509	0.563	0.659	0.52	0.608
10-19.9 cm	0.368	0.348	0.251	0.412	0.303
20+ cm	0.123	0.089	0.09	0.068	0.089
ROCK: Sample Size		9	12	9	31
Mean Abundance Per Sample		186.3	263.3	350.6	260.5
Median Fish Length (cm)		8.8	7.8	8.3	8.2
Proportion Abundance by Length Group					
1-9.9 cm		0.802	0.858	0.79	0.818
10-19.9 cm		0.143	0.122	0.1	0.12
20+ cm		0.055	0.02	0.111	0.063
RUBBLE: Sample Size		12	16	11	41
Mean Abundance Per Sample		234.3	333.5	370.5	326.2
Median Fish Length (cm)		8	6.5	7.7	7.5
Proportion Abundance by Length Group					
1-9.9 cm		0.802	0.927	0.839	0.86
10-19.9 cm		0.151	0.053	0.123	0.11
20+ cm		0.047	0.02	0.038	0.03
Chi-square Tests: Proportion Abundance by Length Group	Coral - Winter	Coral - Spring	Coral - Summer	Coral - Fall	All Coral
Coral - Winter		NS	0.1	NS	NS
Coral - Spring	NS		NS	NS	NS
Coral - Summer	0.1	NS		0.06	NS
Coral - Fall	NS	NS	0.06		NS
All Coral	NS	NS	NS	NS	
Chi-square Tests: Proportion Abundance by Length Group		Rock - Spring	Rock-Summer	Rock - Fall	All Rock
Rock - Spring			NS	NS	NS
Rock-Summer		NS		0.04	NS
Rock - Fall		NS	0.04		NS
All Rock		NS	NS	NS	
Chi-square Tests: Proportion Abundance by Length Group		Rubble -Spring	Rubble - Summer	Rubble - Fall	All Rubble
Rubble - Spring			0.04	NS	NS
Rubble - Summer		0.04		0.16	NS
Rubble - Fall		NS	0.16		NS
All Rubble		NS	NS	NS	
Coral-Rock Pairings - Spring, Summer, Fall		0.01	0.01	0.01	
Coral-Rubble Pairings - Spring, Summer, Fall		0.01	0.01	0.01	
Rock-Rubble Pairings - Spring, Summer, Fall		NS	NS	0.14	

season. These results indicate that, while significant seasonal variations in abundance do occur in all complex substrate samples, seasonal differences in fish numbers do not significantly affect size-structure relationships within and between bottom-cover types.

Intrasubstrate Comparisons: The Test for Randomness

To this point, all analysis results suggest that fish populations occupying habitats of very different physical complexity have significantly different size and mass characteristics that fall within relatively narrow ranges. However, these results are based on means constructed across many sample sites from numerous locations. Could random processes possibly account for such results? If homogeneous bottom-cover types have unique fish size ranges that are related to their geometric characteristics, then smaller, location-specific and random subsamples should fall within the cumulative size ranges defined for the aggregate samples. To test this proposition, the original homogeneous bottom-cover samples were expanded to include all sites containing homogeneous mixtures of sand-coral, sand-rock, sand-rubble and sand-grass where the non-sand components were at least 70 percent. These expanded samples were then stratified by forereef and backreef components for specific reef locations. In total, four forereef and two backreef locations were developed from the expanded coral sample, while rock and rubble sample sites yielded two locations in each zone (Table 4.24). Grass samples could not be stratified by location, as practically all sample sites were located in the Looe Key backreef zone. In addition, 30 random samples of ten sites each were drawn from the original samples to test the stability of these size-structure relationships.

Table 4.24. Species characteristics and statistical tests for homogeneous forereef and backreef coral, rock and rubble locations. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

Homogeneous Coral Locations	Molasses Forereef	French Forereef	Looe Key Forereef	Other Forereef	BNP Backreef	Other Backreef
Sample Size	47	11	125	53	61	33
Mean Species Per Sample	24	23.8	23.8	20.1	16.8	16.5
Median Fish Length (cm)	13	10.9	10.7	10	9.4	8.1
Median Species Weight (g)	57.2	37.4	30.4	26.3	20.5	11.1
Chi-square Tests: Proportion by Weight	Molasses Forereef	French Forereef	Looe Key Forereef	Other Forereef	BNP Backreef	Other Backreef
Molasses Forereef		NS	0.12	0.02	0.01	0.01
French Forereef	NS		NS	NS	0.1	0.01
Looe Key Forereef	0.12	NS		NS	NS	0.06
Other Forereef	0.02	NS	NS		NS	NS
BNP Backreef	0.01	0.1	NS	NS		NS
Other Backreef	0.01	0.01	0.06	NS	NS	
Homogeneous Rock Locations	Molasses Forereef	Other Forereef	Other Backreef	Looe Key Backreef		
Sample Size	19	8	7	6		
Species Per Sample	19.4	19.9	17.1	14.3		
Median Fish Length (cm)	8.4	10.6	7.6	7		
Median Species Weight (g)	12.4	24.8	6	10.9		
Chi-square Tests: Proportion by Weight	Molasses Forereef	Other Forereef	Other Backreef	Looe Key Backreef		
Molasses Forereef		NS	0.06	NS		
Other Forereef	NS		0.01	NS		
Other Backreef	0.06	0.01		0.04		
Looe Key Backreef	NS	NS	0.04			
Homogeneous Rubble Locations	Molasses Forereef	Looe Key Forereef	Looe Key Backreef	Other Backreef		
Sample Size	28	9	17	7		
Mean Species Per Sample	22.7	21.6	16.4	20.7		
Median Fish Length (cm)	8.2	8.9	5.1	5.9		
Median Species Weight (g)	14.5	19.9	2.8	4.1		
Chi-square Tests: Proportion by Weight	Molasses Forereef	Looe Key Forereef	Looe Key Backreef	Other Backreef		
Molasses Forereef		NS	0.01	0.01		
Looe Key Forereef	NS		0.01	0.01		
Looe Key Backreef	0.01	0.01		NS		
Other Backreef	0.01	0.01	NS			

Location-Specific Subsamples

This analysis shows that all location-specific cumulative frequency curves for species and abundance for all complex bottom-cover types fall basically within the bounds established in the previous section (Figures 4.25 and 4.26). With the exception of rubble substrata, there appears to be no specific break that separates species sizes for individual locations. Instead, intrasubstrate species size distributions appear to move smoothly across a continuum within the bounding ranges, as do median fish lengths and weights (Table 4.24). In most cases, forereef locations occupy the center to right side of the range while backreef locations occupy the left side of the range. Size structures for locations on opposite sides of the bounding distributions tend to display significant statistical differences between themselves but not in pairings with locations whose size structures lie towards the middle.

Perhaps because of the large sample size, homogeneous coral locations show the smoothest relative transition in species size characteristics from forereef to backreef (Table 4.24, Figure 4.25A). Location-specific species size characteristics tend to be significantly different only in pairings at the extremes of the range (Table 4.24). This transition becomes less smooth in abundance as a significant size distinction begins to emerge between two large forereef locations (Molasses and French reefs) and the remaining locations (Figure 4.26A). This is confirmed by chi-square tests that show statistical independence in pairings with all other coral locations (Table 4.25).

Location-specific analyses for rock and rubble substrata are limited by small sample sizes. However, several important results emerge. First, there are no significant differences detected by chi-square tests in species size structure between intrasubstrate pairings of Molasses Reef

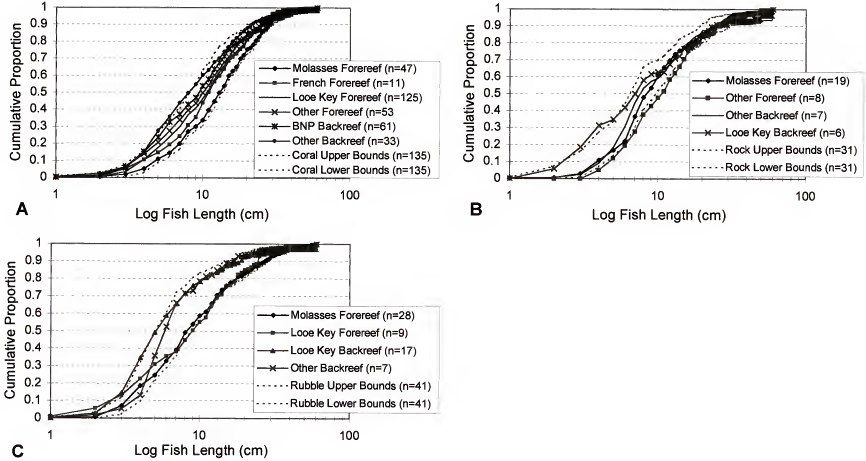

Figure 4.25. Species size-structure relationships between substrate-specific locations overplotted with bounding cumulative frequency curves from Figure 4.19.

A) Species size structure for homogeneous, location-specific coral samples.
B) Species size structure for homogeneous, location-specific rock samples.
C) Species size structure for homogeneous, location-specific rubble samples.

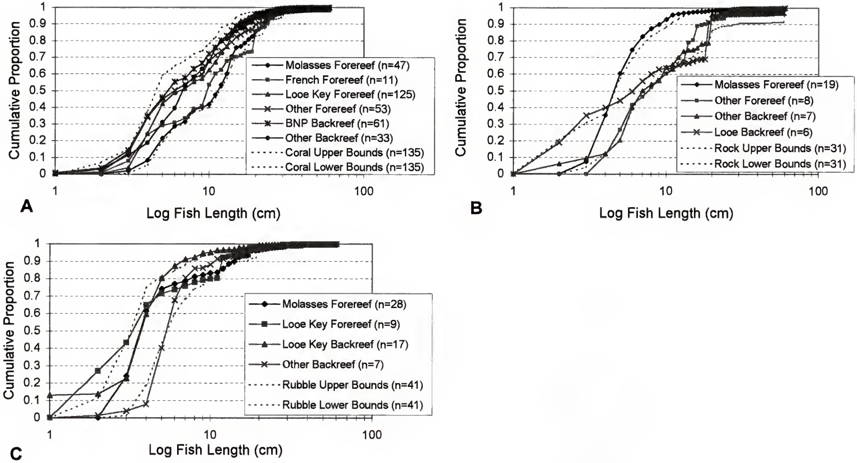

Figure 4.26. Abundance size-structure relationships between substrate-specific locations overplotted with bounding cumulative frequency curves from Figure 4.20.

A) Abundance size structure for homogeneous, location-specific coral samples.
B) Abundance size structure for homogeneous, location-specific rock samples.
C) Abundance size structure for homogeneous, location-specific rubble samples.

Table 4.25. Abundance characteristics and statistical tests for homogeneous forereef and backreef coral, rock and rubble locations. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

Homogeneous Coral Locations	Molasses Forereef	French Forereef	Looe Key Forereef	Other Forereef	BNP Backreef	Other Backreef
Sample Size	47	11	125	53	61	33
Mean Abundance Per Sample	336	226.4	314.4	187.8	92	169.2
Chi-square Tests: Proportion Abundance by Length Group	Molasses Forereef	French Forereef	Looe Key Forereef	Other Forereef	BNP Backreef	Other Backreef
Molasses Forereef		NS	0.01	0.02	0.01	0.01
French Forereef	NS		0.01	0.02	0.01	0.01
Looe Key Forereef	0.01	0.01		0.1	0.18	NS
Other Forereef	0.02	0.02	0.1		NS	0.16
BNP Backreef	0.01	0.01	0.18	NS		NS
Other Backreef	0.01	0.01	NS	0.16	NS	
Homogeneous Rock Locations	Molasses Forereef	Other Forereef	Other Backreef	Looe Backreef		
Sample Size	19	8	7	6		
Mean Abundance Per Sample	325.894	145	146.142	82.3333		
Chi-square Tests: Proportion Abundance by Length Group	Molasses Forereef	Other Forereef	Other Backreef	Looe Backreef		
Molasses Forereef		0.01	0.01	0.01		
Other Forereef	0.01		0.02	NS		
Other Backreef	0.01	0.02		0.05		
Looe Backreef	0.01	NS	0.05			
Homogeneous Rubble Locations	Molasses Forereef	Looe Key Forereef	Looe Key Backreef	Other Backreef		
Sample Size	28	9	17	7		
Mean Abundance Per Sample	351.785	325.111	226.823	133.571		
Chi-square Tests: Proportion Abundance by Length Group	Molasses Forereef	Looe Key Forereef	Looe Key Backreef	Other Backreef		
Molasses Forereef		NS	0.03	NS		
Looe Key Forereef	NS		0.01	NS		
Looe Key Backreef	0.03	0.01		0.11		
Other Backreef	NS	NS	0.11			

forereef sample sites and other forereef locations for either rock or rubble substrata (Table 4.24). This is important since it demonstrates that rock and rubble samples collected from the grounding site of the freighter M/V Wellwood, which constitute 58 and 54 percent respectively of all such homogeneous sites, have species size structures that are not significantly different from other forereef rock and rubble locations. However, median species weights are higher in non-Molasses forereef locations (Table 4.24). These differences are greatest at forereef rock sites whose constituent geometry may largely reflect the remnants of dead and eroded coral formations. Here, Molasses forereef locations have species assemblages whose median weight is only half that of other forereef rock sample sites and whose abundance concentrations contain much smaller proportions of medium and large-sized fishes. In fact, these sites represent the only set of rock samples where the abundance of medium and large-sized fishes are significantly lower than similarly-located rubble sites. This suggests that bottom covers at the grounding site were more thoroughly pulverized and abraded than more natural rock and rubble locations. This would be particularly true of remnant coral structures where most of the larger natural spaces may have been eliminated by the grounding.

Differences in the geometric characteristics of rock and rubble substrata may also explain a second result of this analysis, namely, that forereef and backreef rock sample sites display much greater similarities in their species size structures than similarly-located rubble samples (Table 4.24). Mechanical grading occurs in sediment sizes as detrital material is transported. Thus, the very large differences observed between species size structures in forereef and backreef rubble locations (Figure 4.25) may simply reflect the expected differences in the geometry of detrital materials between zones, while dead and eroding coral remnants may have greater interzonal similarity.

Random Subsamples

If further evidence is needed to support the contention that the observed fish-population size structures are not the result of random events, then analysis of randomly selected sample sites from each of the complex bottom covers provides it. Thirty samples of ten sites each were selected from the master sample sets for each complex bottom cover using a random number generator in an Excel spreadsheet. Cumulative size curves were constructed and compared to the bounding size curves developed from confidence intervals. Results indicate that none of these random sample aggregations for coral, rock and rubble substrata have median species lengths that fall outside of the bounding size curves (Figures 4.27A, B and C). Grass bottom covers show different results. Fully 43 percent of these random subsamples have cumulative frequency curves whose median values lie outside of the bounding size range (Figure 4.27D). This results primarily from the inclusion of small to median-sized schools of non-resident grunts in a large minority of the grass sample sites. Large numbers of these reef-related invertivores forage in nearby sea grass beds and seriously skew the cumulative size curves of many random samples in the 8 to 20 cm size range.

Cumulative frequency curves of abundance for random subsamples show the same general pattern as species but with a slightly larger number of statistical outliers. A total of 17, 27 and 20 percent of the random subsamples for coral, rock and rubble display cumulative frequency curves whose median values are smaller than the lower bounding size range. None had median values that were larger than the upper bound (Figure 4.28). While most of these differences were very small, several subsamples in coral and rubble bottom covers were seriously skewed to smaller sizes by the occurrence of a few, very large schools of small fishes in the 2 to 3-cm

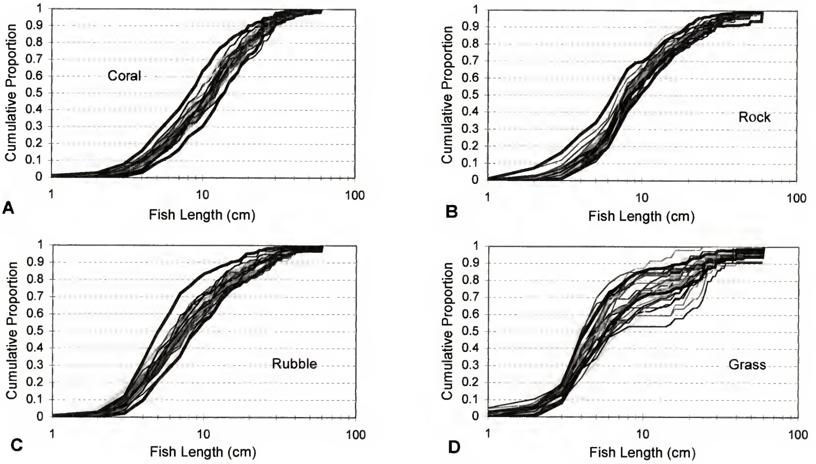

Figure 4.27. Cumulative frequency of all species by fish length for 30 random samples of 10 sites each in homogeneous coral, rock, rubble and grass bottom covers overplotted with bounding cumulative frequency curves (wide black lines) from Figure 4.20. A) Cumulative frequency curves for random coral samples. B) Cumulative frequency curves for random rock samples. C) Cumulative frequency curves for random rubble samples. D) Cumulative frequency curves for random grass samples.

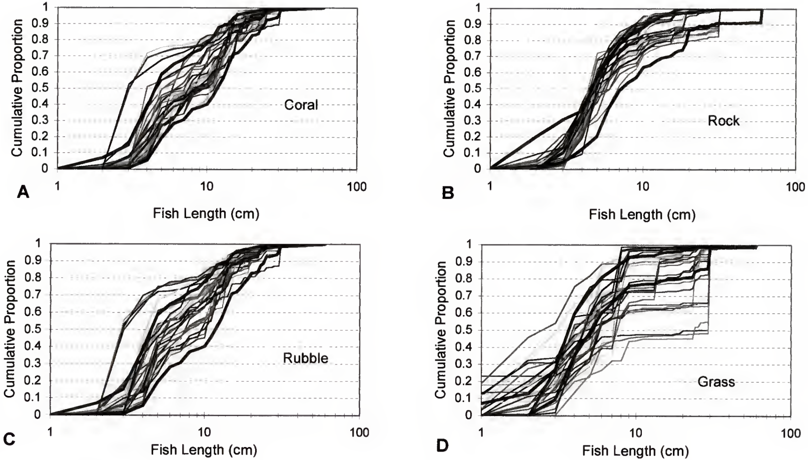

Figure 4.28. Cumulative frequency of abundance by fish length for 30 random samples of 10 sites each for homogeneous bottom-cover types overplotted with bounding cumulative frequency curves (wide black lines) from Figure 4.21. A) Cumulative frequency curves for random coral samples. B) Cumulative frequency curves for random rock samples. C) Cumulative frequency curves for random rubble samples. C) Cumulative frequency curves for random grass samples.

size range (Figures 4.28A and C). Grass bottom covers show the same large discrepancies as in species. Large, non-resident schools of grunts occur in many sample sites, seriously skewing the cumulative size curves of many random subsamples in the 8 to 20 cm length ranges.

Assessment of the Stochastic Hypothesis

While a small proportion of the random abundance samples fall outside the established confidence intervals, it is still possible to state with confidence that the significant differences observed in fish-population size structures between bottom-cover types are not the result of random events. Multiple random and location-specific subsamples in coral, rock and rubble bottom covers consistently display statistically-similar intrasubstrate size distributions. Minor adjustments to the lower bounding size curves for abundance in these substrata would eliminate most of the statistical outliers without affecting the intersubstrate size-range relationships. Removal of non-resident fish observations from grass sample sites would seriously reduce the variance in these size curves. In light of these results, the stochastic null hypothesis cannot be rejected.

The Trophic Composition of Reefscapes: A Test for Causality

There seems little doubt that food is an important factor in explaining the concentrations of coral-reef fishes which have been shown to increase directly with substrate complexity. Changes in the spatial concentrations of specific food sources such as plankton, algae and marine invertebrates must have some effect on the concentrations of fishes that specialize in such food sources. Can fish-population size-structure changes be attributed to shifts in the proportional concentrations of trophic groups between substrate types? Such a thesis requires that trophic groups have unique size distributions which may overlap, but whose mean and median size properties are significantly different.

The Trophic Composition of Species

Comparisons of trophic composition between the five homogeneous substrate types show no significant differences in the mean number of species (Table 4.26, Figure 4.30A) or in proportional representation (Figure 4.30C) of the four major trophic classes (planktivores, herbivores, invertivores and piscivores) between coral, rock and rubble substrata. Rock and rubble do have slightly fewer planktivore species and slightly more herbivore species than coral substrata, but these are not significant (Table 4.26). The lower overall mean species value for rock substrata is proportioned across all four classes. There are, however, significant differences in trophic composition between grass, sand and the more-complex substrate types (Table 4.26, Figure 4.30C). The proportional representation of herbivores declines by 17 and 37 percentage points in grass and sand respectively, while invertivores increase by nearly similar amounts.

All trophic classes show the same overall shift in species size across the complexity gradient as were observed for all species. This is demonstrated in the cumulative frequency curves displayed in Figure 4.29. Median species lengths (Figure 4.30B) and weights (Figure 4.30D) display the same two-step decline from coral to rock-rubble to grass-sand for all trophic classes except piscivores. Grass bottom covers contain four occurrences of one large, transient planktivore species (Inermia vittat) which skew the results by length but are excluded from median weight values because a weight-to-length relationship could not be established for this species. The proportion of species concentrated in the smallest length grouping (1-9.9 cm)

Table 4.26. Species characteristics by trophic class by substrate type.

	All Coral	All Rock	All Rubble	All Grass	All Sand
Sample Size	135	31	38	41	21
Mean Species Per Sample					
Planktivore	1.7	0.9	1.2	0.1	0.1
1-9.9 cm	0.9	0.6	1	0	0.1
10-19.9 cm	0.8	0.3	0.2	0	0
20+ cm	0	0	0	0.1	0
Herbivore	8.2	8.3	9	1.3	0.1
1-9.9 cm	3.7	4.7	5.3	1.1	0.1
10-19.9 cm	3.1	2.5	2.3	0.1	0
20+ cm	1.4	1.1	1.5	0.1	0
Invertivore	7.4	6.7	7.3	2.7	1.1
1-9.9 cm	3.1	4.3	5.1	2.3	1
10-19.9 cm	3	1.9	1.6	0.2	0.1
20+ cm	1.2	0.6	0.6	0.2	0
Piscivore	2.4	1.9	2.4	0.9	0.3
1-9.9 cm	0.3	0.4	0.4	0.3	0.1
10-19.9 cm	0.5	0.5	0.8	0.2	0
20+ cm	1.6	1.1	1.1	0.5	0.1
Proportion of All Species					
Planktivore	0.082	0.048	0.058	0.024	0.088
Herbivore	0.395	0.439	0.44	0.262	0.059
Invertivore	0.354	0.357	0.356	0.519	0.676
Piscivore	0.113	0.103	0.115	0.181	0.176
Median Fish Weight (grams)					
Planktivore	22.6	10.3	10.3	1	0.6
Herbivore	27.6	9.9	9.4	2	0.4
Invertivore	30.6	8.6	5.5	1.5	1.5
Piscivore	179.8	121	104.5	158.5	120.1
Proportion Species by Length Group					
Planktivore					
1-9.9 cm (Planktivore)	0.52	0.679	0.816	0.2	1
10-19.9 cm (Planktivore)	0.48	0.321	0.163	0.2	0
20+ cm (Planktivore)	0	0	0.02	0.6	0
Herbivore					
1-9.9 cm (Herbivore)	0.455	0.568	0.586	0.8	1
10-19.9 cm (Herbivore)	0.38	0.304	0.251	0.091	0
20+ cm (Herbivore)	0.165	0.128	0.162	0.109	0
Invertivore					
1-9.9 cm (Invertivore)	0.423	0.632	0.703	0.872	0.87
10-19.9 cm (Invertivore)	0.412	0.278	0.22	0.064	0.087
20+ cm (Invertivore)	0.165	0.091	0.077	0.064	0.043
Piscivore					
1-9.9 cm (Piscivore)	0.113	0.2	0.175	0.289	0.333
10-19.9 cm (Piscivore)	0.208	0.233	0.351	0.184	0.167
20+ cm (Piscivore)	0.679	0.567	0.474	0.526	0.5

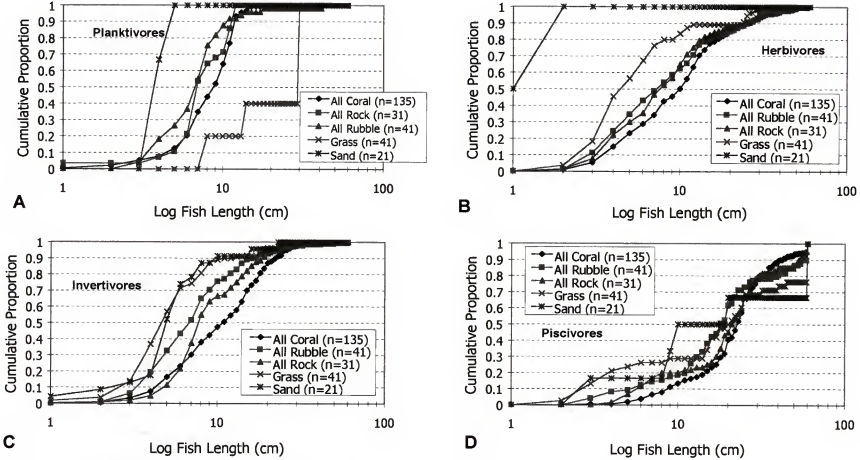

Figure 4.29. Cumulative frequency of all species by trophic class by fish length for homogeneous bottom-cover types. A) Cumulative frequency of planktivores. B) Cumulative frequency of herbivores. C) Cumulative frequency of invertivores. D) Cumulative frequency of piscivores.

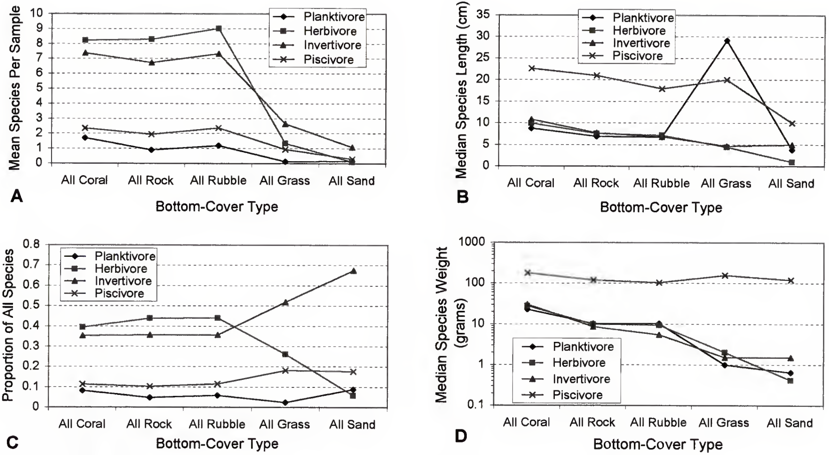

Figure 4.30. Species characteristics by trophic class for homogeneous bottom-cover types. A) Mean species per sample by trophic class. B) Median species length by trophic class. C) Proportion of all species by trophic class. D) Median species weight by trophic class.

doubles for planktivores, herbivores and invertivores (Figure 4.31A), while those in the middle grouping (10-19.9 cm) decline to very small values (Figure 4.31B). The largest length grouping (20-plus cm) also shows a proportional decline, but not as great (Figure 4.31C).

Median species lengths and weights are not significantly different for planktivores, herbivores and invertivores at any point along the substrate transition (Figures 4.30B and D) with the one exception noted for grass. Piscivores are 2 to 4 times the length (Figure 4.30B) and 4 to 100 times the weight (Figure 4.30D) of the other trophic classes. Since piscivores are considered less dependent on shelter provided by the substrata, they might be expected to show the smallest size changes. This is only partially true. While median weights are relatively similar across the complexity gradient, mean piscivore lengths do show a shift to smaller values. This inconsistency is explained by the fact that length-to-weight relationships could not be established for many of the larger piscivores. Species proportions in the smallest and largest length groupings display the same general slope as the other trophic classes (Figures 4.31A and C). However, unlike the other classes, there is very little change in the middle length group (Figure 4.31B). It would appear that as fishes in other trophic classes shift into the smallest length grouping, piscivore sizes shift to the middle length group.

Statistical tests confirm the significance and similarity of these size shifts. Chi-square tests conducted on species percentages by length group for each trophic class (Table 4.27) indicate statistical independence for all substrate sample pairings except for coral-rock in herbivores, rock-rubble in herbivores, invertivores and piscivores, grass-sand in invertivores and piscivores and rock-grass in piscivores. K-S statistics (Table 4.28) computed on cumulative frequency curves (Figure 4.29) show the same results plus some differences. Here, all herbivore pairings

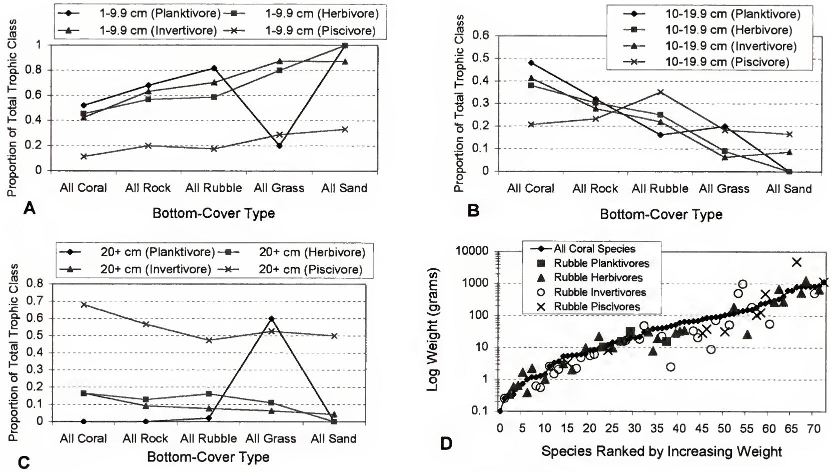

Figure 4.31. Distribution of species by trophic class and size grouping for homogeneous bottom-cover types.
A) Proportion of trophic-class species in the 1-9.9 cm length group.
B) Proportion of trophic-class species in the 10-19.9 cm length group.
C) Proportion of trophic-class species in the 20-plus cm length group.
D) Distribution of species by trophic class and median weight: coral and rubble substrata.

Table 4.27. Significance levels of chi-square statistical tests of species by trophic class for homogeneous substrate types. Numbers represent significant alpha levels below 0.20. NS equals 'not significant'.

Chi-square Tests: Proportion of All Species	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		NS	NS	0.02	0.01
All Rock	NS		NS	0.02	0.01
All Rubble	NS	NS		0.02	0.01
All Grass	0.02	0.02	0.02		0.01
All Sand	0.01	0.01	0.01	0.01	
Chi-square Tests: Proportion Species by Length Group	All Coral	All Rock	All Rubble	All Grass	All Sand
Planktivores					
All Coral		0.03	0.01	0.01	0.01
All Rock	0.03		0.02	0.01	0.01
All Rubble	0.01	0.04		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	
Herbivores					
All Coral		NS	0.12	0.01	0.01
All Rock	NS		NS	0.01	0.01
All Rubble	0.12	NS		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	
Invertivores					
All Coral		0.02	0.01	0.01	0.01
All Rock	0.02		NS	0.01	0.01
All Rubble	0.01	NS		0.01	0.02
All Grass	0.01	0.01	0.01		NS
All Sand	0.01	0.01	0.02	NS	
Piscivores					
All Coral		0.17	0.02	0.04	0.01
All Rock	0.17		0.19	NS	0.09
All Rubble	0.02	0.19		0.02	0.01
All Grass	0.04	NS	0.02		NS
All Sand	0.01	0.09	0.01	NS	

Table 4.28. Significance levels of Kolmorov-Smirnov (K-S) statistical tests of species by trophic class for homogeneous substrate types. Numbers represent significant alpha levels below 0.20. NS equals 'not significant'.

	All Coral	All Rock	All Rubble	All Grass	All Sand
Planktivores					
All Coral		0.13	0.01	0.01	0.01
All Rock	0.13		NS	0.01	0.01
All Rubble	0.01	NS		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	
Herbivores					
All Coral		NS	NS	0.01	0.01
All Rock	NS		NS	0.03	0.01
All Rubble	NS	NS		0.05	0.01
All Grass	0.01	0.03	0.05		0.01
All Sand	0.01	0.01	0.01	0.01	
Invertivores					
All Coral		0.11	0.01	0.01	0.01
All Rock	0.11		0.19	0.01	0.01
All Rubble	0.01	0.19		0.04	0.07
All Grass	0.01	0.01	0.04		NS
All Sand	0.01	0.01	0.07	NS	
Piscivores					
All Coral		NS	0.06	0.04	0.01
All Rock	NS		NS	NS	0.11
All Rubble	0.06	NS		NS	0.06
All Grass	0.04	NS	NS		NS
All Sand	0.01	0.11	0.06	NS	

between coral, rock and rubble as well as all piscivore pairings between adjacent substrate types are not significant.

With the exception of planktivores, species in specific trophic classes do not display any dramatic clustering in particular parts of the size spectrum (Figure 4.31D). Instead, they appear to occur as a series of small clusters extending across the entire size range. This is particularly true of herbivores and invertivores. Piscivores have larger median weights, but some species still occur in the smaller weight groups. As shown in Figure 4.31D, the transition from coral to rubble substrata result in a shift of practically all shared species weighing 30 to 300 grams, regardless of trophic class, to smaller or larger sizes. This suggests that whatever factor is responsible for the size shifts, it seems to affect all trophic classes equally.

The Taxonomic Composition of Species

Analysis of taxonomic families by bottom-cover type yields the same general results as trophic classes. Species in 18 families constitute 90 to 95 percent of occurrences in coral, rock and rubble sample sites. There are differences in the proportional family composition of coral substrata when compared to rock and rubble. Corals have larger proportional concentrations (37 percent versus 25 percent) of damselfishes (Pomacentridae), grunts (Haemulidae) and butterflyfishes (Chaetodontidae), while wrasses (Labridae) and parrotfishes (Scaridae) are proportionately more important in rock and rubble substrata, constituting 37 and 38 percent respectively versus 28 percent in corals (Table 4.29). Even with these differences, chi-square tests show that the percentage distribution of species among the top ten families are not significantly different between coral, rock and rubble substrata.

Table 4.29. Taxonomic family characteristics for coral, rock and rubble substrata sorted in descending order by number of sample occurrences in coral bottom covers.

	Median Fish Length (cm)			Median Fish Weight (grams)		
Common Family Name	Coral	Rock	Rubble	Coral	Rock	Rubble
Damselfishes	7.7	7	5.7	11.8	9.8	3.6
Wrasses	8	7.8	7	2.6	4.1	2.1
Parrotfishes	16.3	10.2	14.5	45.7	8.8	20.4
Grunts	16.4	15.8	13	94.6	67.5	43
Surgeonfishes	12.5	11.3	9.5	48.9	29.7	16.4
Sea Basses	10	8	6.5	11.9	8.2	5.4
Snappers	23	21.5	20	219.4	180.3	131.8
Butterflyfishes	9	8	9	21.7	16.7	19.2
Angelfishes	18.5	16	13	192.7	237.5	89.5
Jacks	19.5	20	14.5	120.2	154.5	47.3
Gobies	3	3.8	3.5	0.3	0.3	0.7
Leatherjackets	27	46	10	277.2	853.4	157.9
Squirrelfishes	17	19.5	13	104.1	133.2	104.1
Drums	12		11	18.5		14.2
Puffers	4.5	4.5	3	1.5	1.5	1.2
Goatfishes	24	21	16	279.3	159.7	54.5
Trumpetfishes	35	28	23	105.2	55.5	35.8
Barracudas	55	54	55	1149.9	1087.9	4448.7
	Species Per Sample			Proportion of All Species		
Common Family Name	Coral	Rubble	Rock	Coral	Rubble	Rock
Damselfishes	4.3	3.2	2.8	0.206	0.15	0.15
Wrasses	2.7	3.8	3.5	0.131	0.176	0.188
Parrotfishes	3.1	4.2	3.7	0.147	0.198	0.197
Grunts	2.5	1.6	1.4	0.119	0.076	0.072
Surgeonfishes	1.7	1.9	1.6	0.08	0.089	0.085
Sea Basses	0.9	1.1	1.2	0.044	0.05	0.063
Snappers	1.2	1	0.7	0.059	0.046	0.039
Butterflyfishes	0.9	0.6	0.6	0.041	0.026	0.031
Angelfishes	0.7	0.5	0.6	0.035	0.025	0.032
Jacks	0.4	0.3	0.3	0.019	0.015	0.014
Gobies	0.3	0.7	0.8	0.014	0.031	0.043
Leatherjackets	0.2	0.1	0.3	0.011	0.003	0.014
Squirrelfishes	0.2	0	0.1	0.011	0.002	0.003
Drums	0.2	0	0	0.008	0.001	0
Puffers	0.2	0	0.1	0.011	0.002	0.003
Goatfishes	0.2	0.4	0.2	0.011	0.017	0.012
Trumpetfishes	0.2	0.2	0.2	0.012	0.008	0.009
Barracudas	0.1	0.4	0.3	0.006	0.017	0.014

Like trophic composition, there are significant differences in the size structure of family assemblages between bottom covers. Of the 18 top families, 13 have larger median lengths and 10 have heavier weights in coral than in rock substrata, while 15 have larger lengths and weights than in rubble (Table 4.29). These include the top nine families, which account for 85 percent of all specie occurrences in coral bottom covers. Those with smaller weights in corals than in rock are primarily larger piscivores, browsers and invertivores: angelfishes (Pomacanthidae), jacks (Carangidae), leatherjackets (Balistidae) and squirrelfishes (Holocentridae).

Trophic Composition and Abundance

Comparisons of trophic composition by abundance between the five homogeneous substrate types show certain specific differences from species. While species comparisons indicated no significant differences between the three more-complex substrate types, analysis of mean abundance indicates that coral substrata are significantly different from rock and rubble in terms of mean and proportional abundance in two trophic classes (Table 4.30, Figure 4.32A). Planktivores decline from 21.5 percent of total abundance in coral substrata to 3 and 9 percent respectively in rock and rubble. Herbivores increase from 27 percent of total abundance to 53.7 and 55.2 percent respectively. One-way ANOVAs show no significant differences between invertivores and piscivores although mean abundance does decline from coral to rock and rubble.

With one exception, all trophic classes display the same shift in fish-abundance size structure across the complexity gradient as were observed for species trophic composition. Planktivores show no significant differences in size structure between coral, rock and rubble substrata (Table

Table 4.30. Characteristics and statistical tests of abundance by trophic class for homogeneous bottom-cover types. Chi-square values represent significant alpha levels below 0.20. NS equals 'not significant'.

	All Coral	All Rock	All Rubble	All Grass	All Sand
Sample Size	135	31	41	41	21
Mean Abundance Per Sample					
Planktivore	65.6	7.9	26	13.2	0.4
1-9.9 cm	37.5	4.7	15.1	3.7	0.4
10-19.9 cm	28	3.3	10.9	1.7	0
20+ cm	0	0	0	7.8	0
Herbivore	82.2	140	158.7	9.3	0.1
1-9.9 cm	58.4	124.1	145.9	8.2	0.1
10-19.9 cm	18.2	14	9.1	0.2	0
20+ cm	5.6	1.9	3.7	0.9	0
Invertivore	133.9	96.6	119.6	21.3	14
1-9.9 cm	87	82.6	109.5	20.5	13.4
10-19.9 cm	40.9	12.3	8.5	0.2	0.5
20+ cm	6	1.6	1.5	0.6	0
Piscivore	19.7	5	11.2	2	0.4
1-9.9 cm	0.9	0.6	1	1	0
10-19.9 cm	4	1.1	5.9	0.3	0.2
20+ cm	14.9	3.2	4.3	0.6	0.1
Proportion of All Abundance					
Planktivore	0.215	0.03	0.09	0.287	0.026
Herbivore	0.27	0.537	0.552	0.204	0.006
Invertivore	0.439	0.371	0.416	0.465	0.942
Piscivore	0.065	0.019	0.039	0.043	0.026
Median Fish Length (cm)					
Planktivore	8.8	6.9	6.7	29.2	3.8
Herbivore	9.9	7.6	7.2	4.4	1
Invertivore	10.8	7.7	6.8	4.7	4.9
Piscivore	22.6	21	17.9	20	10
Chi-square Tests: Proportion of All Abundance	All Coral	All Rock	All Rubble	All Grass	All Sand
All Coral		NS	NS	0.01	0.01
All Rock	NS		NS	0.01	0.01
All Rubble	NS	NS		0.01	0.01
All Grass	0.01	0.01	0.01		0.01
All Sand	0.01	0.01	0.01	0.01	

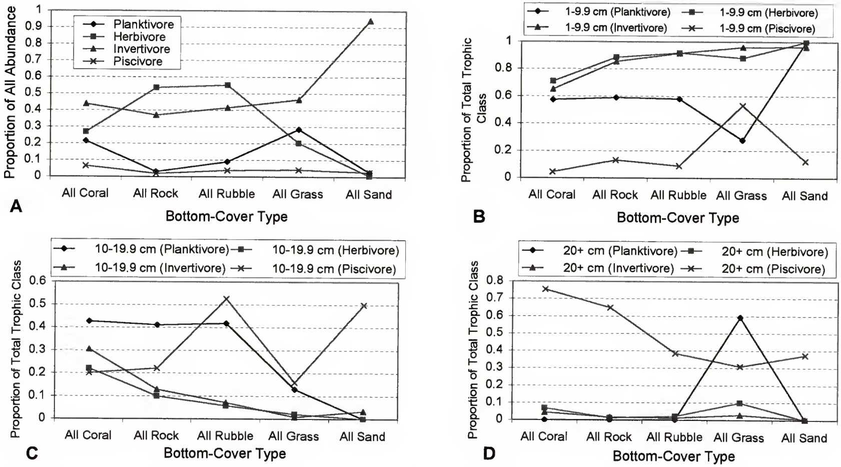

Figure 4.32. Characteristics of abundance by trophic class for homogeneous bottom-cover types. A) Proportion of total abundance by trophic class. B) Proportion of trophic-class abundance in the 1-9.9 cm length group. C) Proportion of trophic-class abundance in the 10-19.9 cm length group. D) Proportion of trophic-class abundance in the 20-plus cm length group.

4.30). Proportional concentrations of abundance in each length group are essentially the same. Otherwise, concentrations of abundance in the smallest length grouping increase across the gradient while concentrations in the middle and largest length groupings decline (Figures 4.32B, C and D). As in species, planktivore distributions in grass bottom covers are distorted by the sporadic occurrence of the large, transient species Inermia vittat. Piscivores show a large change in abundance concentrations from the largest length group (20-plus cm) to the middle length group (10-19.9 cm).

Assessment of the Trophic Hypothesis

Fish assemblages occurring in the five homogeneous bottom-cover types have been shown to have different trophic characteristics that are undoubtedly related to the distribution of food sources within reefscapes. While complex bottom covers have statistically similar trophic concentrations when measured by mean species occurrences per sample, they are statistically different when measured by mean trophic abundance per sample. Coral bottom covers have greater proportional concentrations of planktivores, while rock and rubble substrata have larger proportional concentrations of herbivores. While grass trophic assemblages are statistically similar to coral bottom covers, sand substrata are overwhelmingly dominated by invertivores.

However, trophic differences between bottom-cover types do not explain the observed differences in species and abundance size structure. Planktivores, herbivores and invertivores have statistically-similar median lengths and weights in each bottom-cover type which become progressively and significantly smaller across the complexity gradient defined for this study. The mechanics of these size shifts are the same as those observed in the aggregate analysis. Given these results, the trophic null hypothesis cannot be rejected.

Dominant Species: A Test of Success

Similarity-index comparisons have shown that the assemblages of species occupying different bottom-cover types are characterized by significant differences in the proportional concentrations of species occurrences and abundance. Such changes could infer that competition plays a major role in structuring the size distributions observed in different substrata. While the trophic composition of species and abundance appears to have no effect on size structure, perhaps changes in the assemblages of dominant species may account for the observed size-structure differences. To test this proposition, a subset of dominant species was selected for each bottom cover based on a listing of substrate-specific species ranked by the number of occurrences normalized by sample size. Species accounting for the top 50 percent of occurrences were selected to represent the dominant species in each bottom-cover type.

This stratification resulted in the selection of 16, 13, 15 and 6 dominant species respectively for coral, rock, rubble and grass substrata (Table 4.31). All dominant species in each of the three non-coral sample sets also occur in coral bottom covers. Only their occurrence frequency and mass characteristics change. Thirteen of the 16 dominant coral species are also dominant in rubble bottom covers, while 11 are dominant in rock substrata (Table 4.31). Only one of six dominant grass species is also dominant in coral. As in the aggregate analysis, dominant species in coral bottom covers include a larger proportion of planktivores and slightly lower proportions of herbivore and invertivore species. Indicative of these differences are the absences of two species from the rock and rubble listings: a coralivore, Chaeton capistratus (the Foureye butterflyfish) and a planktivore, Abudefduf saxatilis (the Sergeant major).

Table 4.31. Characteristics of dominant species for coral, rock and rubble bottom-cover types. Dominant was defined as species accounting for the top 50 percent of all occurrences. Blank cells indicate species not meeting this minimum. Trophic class abreviations are as follow: P=planktivore, H=herbivore, MI=micro-invertivore, MA=macro-invertivore, F=piscivore.

			Weight (grams)			Mean Occurrences Per Sample			Mean Abundance Per Sample		
Species	Common Name	Trophic	Coral	Rock	Rubble	Coral	Rock	Rubble	Coral	Rock	Rubble
Thalassoma bifasciatum	Bluehead	MA	1.2	1.6	0.6	0.93	0.97	0.8	71.3	71.7	57.8
Pomacentrus partitus	Bicolor damselfish	H	1.4	1.4	1.4	0.89	0.97	0.83	32.9	84.4	108.3
Halichoeras maculipinna	Clown wrasse	MA	3.6	3.6	2.1	0.42	0.71	0.76	1.5	4.1	6.2
Scarus croicensis	Striped parrotfish	H	5.6	5.6	2	0.41	0.84	0.9	2.3	15.5	15.6
Halichoeras garnoti	Yellowhead wrasse	MA	5.8	5.8	2.2	0.45	0.74	0.71	1.4	2.2	2.6
Halichoeras bivittatus	Slippery Dick	MA		6	2.6		0.61	0.78		1.8	13.3
Serranus tigrinus	Harlequin bass	MI			5.5			0.49			0.9
Chromis cyanea	Blue chromis	P	10.3		10.3	0.53		0.54	2.7		2.9
Pomacentrus planifrons	Threespot damselfish	H	14.4			0.6			13.5		
Chaetodon capistratus	Foureye butterflyfish	MI	16.7			0.45			0.9		
Sparisoma aurofrenatum	Redband parrotfish	H	30.9	8.8	27.2	0.81	1	0.63	2.8	4.7	2.1
Acanthurus bahianus	Ocean surgeon	H	38.5	22.4	7.7	0.65	0.87	0.95	2.6	17.5	15.6
Abudefduf saxatilis	Sergeant major	P	42.5			0.7			21.7		
Microspathodon chrysurus	Yellowtail damselfish	H	50.8		29	0.74		0.59	4.6		1.6
Acanthurus coeruleus	Blue tang	H	59.7	47.5	42.4	0.8	0.61	0.88	8.9	1.1	3.1
Haemulon flavolineatum	French grunt	MA	67.5	54.3	33.4	0.59	0.52	0.73	4.6	1.8	2.4
Haemulon plumieri	White grunt	MA		93.9			0.48			7	
Sparisoma viride	Stoplight parrotfish	H	116.5	75.5	158.5	0.73	0.65	0.66	2.3	1.6	1.7
Ocyurus chrysurus	Yellowtail snapper	F	180.3	180.3	104.5	0.68	0.65	0.83	4.7	2.2	5.2
Total of Dominant Species						10.38	9.62	11.08	178.7	215.6	239.3
Proportion of all Species or Abundance						0.499	0.509	0.523	0.586	0.828	0.734
Planktivores (Proportion of Dominant)		P				0.118	0	0.049	0.137	0	0.012
Herbivores		H				0.542	0.514	0.491	0.391	0.579	0.618
Invertivores		MI-MA				0.274	0.419	0.385	0.446	0.411	0.348
Piscivores		F				0.066	0.068	0.075	0.026	0.01	0.022

Results indicate that dominate species account for a very large proportion of total abundance and are concentrated in weight sizes ranging from 1 to 300 grams. These species are rather evenly spaced across the size range in coral bottom covers but become concentrated into smaller sizes in rock and rubble substrata. While rock and rubble samples have essentially the same mean number of species as coral samples, occurrences and abundance are systematically concentrated into fewer species. While non-dominant species account for 41.4 percent of all abundance in coral samples, they account for only 18.3 and 26.9 percent of all abundance respectively in rock and rubble samples (Table 4.32). This suggests, perhaps, that the lower structural complexity of rock and rubble habitats allow the same number of species to more thoroughly dominate the reefscape, although they do not totally exclude the other species.

Both dominant and non-dominant species show the same overall shift in the size structure of occurrences and abundance across the complexity gradient as were observed for the aggregate assemblages. Median lengths and weights of dominant species are smaller, but the same trends are observed in both subsets (Table 4.32). There is an increasing proportional concentration of species occurrences and abundance in the smallest length group (1-9.9 cm) and a coincident decline in the middle length group (10-19.9 cm). These shifts are significant as evidenced by chi-square tests that show statistical independence for all substrate pairings except rock-rubble in each subclass (Table 4.32). The coral-rock pairing for dominant species occurrences is significant only at the 0.22 level, but it is obvious that median lengths and weights for this pairing are very different.

The mechanics of this size shift in dominant species are essentially the same as those observed in all previous analyses. Dominant coral species in the middle length and weight

Table 4.32. Dominant and non-dominant species characteristics for homogeneous coral, rock and rubble bottom-cover types. Dominant is defined as species accounting for the top 50 percent of all occurrences.

	Coral Dominant Species	Rock Dominant Species	Rubble Dominant Species	Coral Non-Dominant Species	Rock Non-Dominant Species	Rubble Non-Dominant Species
Sample Size	135	31	41	135	31	41
Mean Species Per Sample	10.4	9.6	10.3	10.4	9.3	10.2
1-9.9 cm	5.2	5.6	6.9	3	4.6	5.5
10-19.9 cm	4.2	3.2	2.7	3.7	2.2	2.5
20+ cm	1	0.8	0.7	3.6	2.4	2.3
Mean Fish Length (cm)	10.5	10.2	8.8	17.4	15.1	13.8
Median Fish Length (cm)	9	7.7	6.3	14.6	9	8.3
Proportion Species by Length Group						
1-9.9 cm	0.498	0.584	0.669	0.292	0.502	0.536
10-19.9 cm	0.408	0.332	0.259	0.36	0.24	0.242
20+ cm	0.094	0.084	0.072	0.349	0.258	0.223
Median Species Weight (g)	21	8.2	6	65.3	22.6	13.9
Mean Abundance Per Sample	178.5	215.5	191.7	126.4	45	95.5
Proportion Abundance by Length Group						
1-9.9 cm	0.731	0.886	0.92	0.434	0.489	0.686
10-19.9 cm	0.238	0.101	0.066	0.396	0.208	0.254
20+ cm	0.031	0.013	0.015	0.17	0.303	0.06
Chi-square Tests: Proportion Species by Length Group	Coral Dominant	Rock Dominant	Rubble Dominant	Coral Non-Dominant	Rock Non-Dominant	Rubble Non-Dominant
Coral Dominant		NS	0.05			
Rock Dominant	NS		NS			
Rubble Dominant	0.05	NS				
Coral Non-Dominant					0.04	0.01
Rock Non-Dominant				0.04		NS
Rubble Non-Dominant				0.01	NS	
Chi-square Tests: Proportion Abundance by Length Group	Coral Dominant	Rock Dominant	Rubble Dominant	Coral Non-Dominant	Rock Non-Dominant	Rubble Non-Dominant
Coral Dominant		0.03	0.01			
Rock Dominant	0.03		NS			
Rubble Dominant	0.01	NS				
Coral Non-Dominant					0.01	0.01
Rock Non-Dominant				0.01		0.01
Rubble Non-Dominant				0.01	0.01	

groups decline in size, occur less frequently and have fewer individuals in rock and rubble substrata, while the smallest species occur more frequently and have greater abundance (Table 4.31). All dominant coral species with median weights of less than 10 grams are also dominant in rock and rubble samples as compared to only half of those weighing more than 10 grams. While the smallest dominant shared species experience increased occurrences and abundance, the larger shared dominants show weight losses, fewer occurrences and less abundance (Table 4.31). Those that disappear from the dominant list still occur in rock and rubble substrata, but at much reduced frequencies. In their place, two new dominant species emerge in the smallest weight group.

It seems obvious from the analysis that dominant species do not control the patterns of size-structure changes that occur between bottom-cover types. The same size shifts in occurrences and abundance are operating here as were observed in the aggregate samples. Thus, the 'Dominant Species' null hypothesis cannot be rejected.

Fish Size Structure and Substrate Geometry: Tests of the Textural-Discontinuity and Limited Shelter Hypotheses

To this point, it has been shown that fish-population size structure, as measured in median length and weight, increases significantly and directly with substrate complexity across the qualitative gradient established from sand to coral. Size-structure changes are not random, and are not related to trophic composition or dominant species. These increases occur at all measured locations, in all trophic classes, in dominant as well as non-dominant species and in practically all taxonomic groups. It has also been shown that surface area associated with Dahl's (1973) measure of gross reef morphology theoretically increases directly with proportion complex bottom cover and local relief. What remains to be established is a direct linkage between fish size structure and quantitative measures of surface area and the sizes of substrate elements and interstitial spaces, i.e., geometric shelter characteristics. Three analyses will be conducted in an attempt to establish this linkage.

Fish Population Size Structure and Substrate Surface Area

Measures of local relief exist for 649 sample sites in the database. Unfortunately, very few of these sites contain homogeneous substrata or homogeneous mixtures of sand and other complex bottom-cover types. However, the combination of coral and gorgonians (soft corals excluded from the original analysis) form a majority in a large proportion of these samples. A new approach was devised using a new data set consisting of all samples where the coral-gorgonian proportion was greater than that for rock-rubble. Gross coral surface-area estimates were computed for each sample site by combining horizontal and vertical measures. Horizontal area was obtained by multiplying the site-specific coral-gorgonian proportion by the observation cylinder cross-sectional area. This value was then multiplied by maximum local relief to obtain gross surface area. Fish characteristics were summed and compared for six gross coral surface-area subclasses. The average rock-rubble content for these sample sites range from 3.7 to 18.8 percent (Table 4.33). Mean substrate relief increases from 0.4 to 3.1 meters across this surface-area gradient (Table 4.33).

Analysis of fish populations comprising the six surface-area subclasses reveals that median lengths and weights increase progressively across the gradient. Median fish length increases by 10 percent (Table 4.33) while median non-piscivore fish weight increases by 64 percent (Table 4.33, Figure 4.33B). While species weighing less than 10 grams decline, both absolutely and

Table 4.33. Species characteristics and statistical tests for sample sites containing measures of local relief by gross coral surface area subclasses. Gross surface-area estimates were developed by multiplying sample observation cylinder cross-sectional area times the proportion of coral and gorgonian bottom cover at each sample site. This value was then multiplied by maximum vertical relief. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
Coral Sample Size	20	148	143	63	32	21
Mean Relief (meters)	0.4	0.8	1.2	1.7	2.5	3.1
Proportion Coral-Gorgonian	29.3	56.2	68.2	77.2	77	94
Proportion Rock-Rubble	10.5	18.8	15.1	9.6	10.3	3.7
Mean Species Per Sample	19.1	19.8	20.3	21.7	22.5	23.3
Median Fish Length (cm)	10.2	10	10.3	9.9	11.1	11.2
Median Fish Weight (grams)	23.5	27.5	28.3	28.1	31.4	38.5
Mean Non-Piscivore Species Per Sample	15.6	16.4	16.8	17.9	18.3	18.7
Median Non-Piscivore Weight (grams)	16.3	16.7	17.5	16.7	17	27.4
Mean Species Per Sample by Fish Weight						
Less than 10 grams	7	7	6.8	7.4	7.8	6.7
10 to 100 grams	5.1	6.2	6.6	7.2	6.7	7.5
100 to 1000 gram	2.9	2.7	3	3	3.4	3.8
1000 plus gram	0.6	0.4	0.4	0.2	0.4	0.6
Proportion Species by Fish Weight						
Less than 10 grams	0.449	0.431	0.405	0.413	0.425	0.36
10 to 100 grams	0.327	0.379	0.394	0.404	0.366	0.403
100 to 1000 gram	0.186	0.166	0.177	0.169	0.187	0.204
1000 plus gram	0.038	0.024	0.023	0.013	0.022	0.033
Chi-square Tests: Proportion Species by Weight Group	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
<100 sq. meters		NS	NS	NS	NS	NS
100-199 sq. meters	NS		NS	NS	NS	NS
200-299 sq. meters	NS	NS		NS	NS	NS
300-399 sq. meters	NS	NS	NS		NS	NS
400-499 sq. meters	NS	NS	NS	NS		NS
500+ sq. meters	NS	NS	NS	NS	NS	

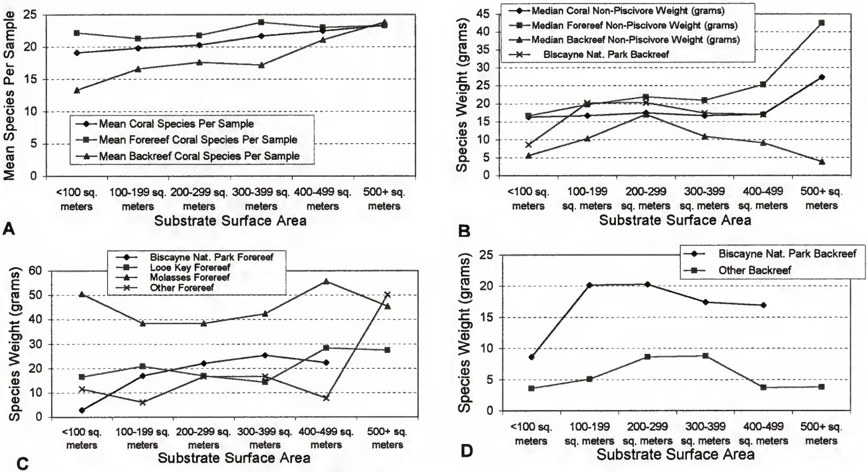

Figure 4.33. Species characteristics for sample sites containing measures of local relief by gross coral surface-area subclasses. A) Mean species per sample by surface-area subclass: all coral sites, forereef coral sites and backreef coral sites. B) Median species weights by surface-area subclass: all coral sites, forereef coral sites and backreef coral sites. C) Median species weights by surface-area subclass: forereef coral locations. D) Median species weights by surface-area subclass: backreef coral locations.

proportionately (Figure 4.34A), species weighing from 10 to 1000 grams increase numerically by 41 percent (Figures 4.34B and C). The largest increases occur in species weighing from 10 to 100 grams, where proportional concentrations shift from 32.7 to 40.3 percent. Chi-square tests conducted on percentage of species by weight group show no statistical independence for any surface-area subclass pairing. While median weight increases dramatically, proportional weight structure across the surface-area range is not significantly different.

Forereef and backreef zones show the same general results as all sample sites. All reef-specific locations (Figure 4.33C and D) show median weight gains across the gradient with the exception of 'other backreef' locations, where the largest surface-area weight observations are abnormally depressed, and seriously affect the overall backreef trends. Over the first two-thirds of the gradient, median forereef and backreef weight relationships have essentially the same slopes (Figures 4.33B). The main difference is that backreef corals have smaller fishes at all points along the transition. While backreef locations in Biscayne National Park have median weights that are closer to normal forereef values, other backreef location values are much smaller (Figure 4.33D). At the opposite extreme, Molasses forereef sites have median weight values that are twice those of other forereef locations (Figure 4.33C). Zonal weight differences are due to slightly greater proportions of species weighing less than 10 grams (Figure 4.34A) and slightly smaller proportions weighing 100 to 1000 grams (Figure 4.34C). While chi-square tests show no significant differences between any forereef pairings (Table 4.34), the smallest surface-area samples are significantly different from larger surface-area samples in backreef locations (Table 4.35), as proportional weight structure becomes closer to that of forereef locations. Mid-range surface-area samples show no significant differences between zones

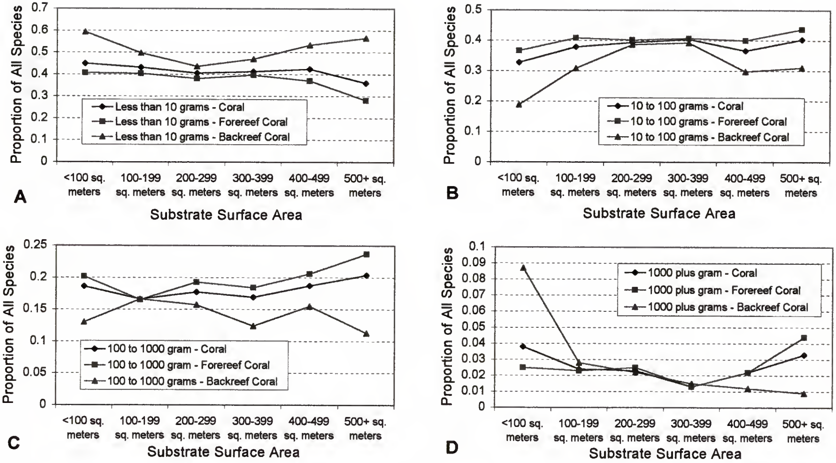

Figure 4.34. Species proportions by weight group by gross coral surface-area subclass for sample sites containing measures of local relief: all coral, forereef coral and backreef coral sample sites.
A) Proportions of all species weighing less than 10 grams. B) Proportions of all species weighing 10 to 100 grams.
C) Proportions of all species weighing 100 to 1000 grams. D) Proportions of all species weighing 1000-plus grams.

Table 4.34. Species characteristics and statistical tests for forereef sample sites containing measures of local relief by gross coral surface area subclasses. Gross surface-area estimates were developed by multiplying sample observation cylinder cross-sectional area times the proportion of coral and gorgonian bottom cover at each sample site. This value was then multiplied by maximum vertical relief. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
Sample Size	13	99	85	43	21	14
Mean Species Per Sample	22.2	21.3	21.8	23.8	23	23.3
Median Fish Length (cm)	10.3	10.3	10.9	10.6	11.5	12.3
Mean Non-Piscivore Species Per Sample	18.7	17.9	18.4	19.8	19.1	19.3
Median Non-Piscivore Weight (grams)	16.7	19.8	21.9	20.9	25.3	42.5
Biscayne Nat. Park Reefs	2.9	16.9	22.1	25.3	22.3	0
Looe Key Reef	16.5	20.9	17	14.3	28.3	27.5
Molasses Reef	50.6	38.5	38.5	42.4	55.7	45.4
Other Reefs	11.5	6	16.7	16.7	7.7	50.1
Mean Species Per Sample by Fish Weight						
Less than 10 grams	7.6	7.2	7	7.8	7.1	5.4
10 to 100 grams	6.8	7.3	7.4	8.1	7.7	8.4
100 to 1000 grams	3.8	3	3.6	3.7	4	4.6
1000 plus grams	0.5	0.4	0.5	0.3	0.4	0.9
Proportion Species by Fish Weight						
Less than 10 grams	0.407	0.404	0.381	0.396	0.371	0.281
10 to 100 grams	0.366	0.408	0.402	0.407	0.4	0.437
100 to 1000 grams	0.202	0.165	0.193	0.184	0.206	0.237
1000 plus grams	0.025	0.023	0.025	0.013	0.022	0.044
Chi-square Tests: Proportion Species by Weight Group	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
<100 sq. meters		NS	NS	NS	NS	NS
100-199 sq. meters	NS		NS	NS	NS	0.18
200-299 sq. meters	NS	NS		NS	NS	NS
300-399 sq. meters	NS	NS	NS		NS	NS
400-499 sq. meters	NS	NS	NS	NS		NS
500+ sq. meters	NS	0.18	NS	NS	NS	

Table 4.35. Species characteristics and statistical tests for backreef sample sites containing measures of local relief by gross coral surface area subclasses. Gross surface-area estimates were developed by multiplying sample observation cylinder cross-sectional area times the proportion of coral and gorgonian bottom cover at each sample site. This value was then multiplied by maximum vertical relief. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
Sample Size	7	47	53	20	10	6
Mean Species Per Sample	13.3	16.6	17.6	17.2	21.1	23.8
Median Fish Length (cm)	10.1	9.6	9.8	9.3	9.7	7.1
Mean Non-Piscivore Species Per Sample	9.9	12.9	14	13.8	16.1	17.7
Median Non-Piscivore Weight (grams)	5.6	10.3	17	10.9	9.1	3.8
Biscayne Nat. Park Reefs	8.6	20.2	20.3	17.4	16.9	
Other Reefs	3.6	5.1	8.6	8.8	3.7	3.8
Mean Species Per Sample by Fish Weight						
Less than 10 grams	5.9	6.4	6.1	6.5	8.6	10
10 to 100 grams	1.9	4	5.4	5.4	4.8	5.5
100 to 1000 grams	1.3	2.1	2.2	1.7	2.5	2
1000 plus grams	0.9	0.4	0.3	0.2	0.2	0.2
Proportion Species by Fish Weight						
Less than 10 grams	0.594	0.498	0.436	0.469	0.534	0.566
10 to 100 grams	0.188	0.308	0.386	0.393	0.298	0.311
100 to 1000 grams	0.13	0.166	0.157	0.124	0.155	0.113
1000 plus grams	0.087	0.028	0.022	0.015	0.012	0.009
Chi-square Tests: Proportion Species by Weight Group	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
<100 sq. meters		0.14	0.01	0.02	NS	NS
100-199 sq. meters	0.14		NS	NS	NS	NS
200-299 sq. meters	0.01	NS		NS	NS	NS
300-399 sq. meters	0.02	NS	NS		NS	NS
400-499 sq. meters	NS	NS	NS	NS		NS
500+ sq. meters	NS	NS	NS	NS	NS	
Backreef (Across) Forereef (down)	<100 sq. meters	100-199 sq. meters	200-299 sq. meters	300-399 sq. meters	400-499 sq. meters	500+ sq. meters
<100 sq. meters	0.01	NS	NS	NS	NS	0.07
100-199 sq. meters	0.01	NS	NS	NS	0.18	0.09
200-299 sq. meters	0.01	NS	NS	NS	0.11	0.04
300-399 sq. meters	0.01	NS	NS	NS	0.14	0.06
400-499 sq. meters	0.01	0.18	NS	NS	0.08	0.02
500+ sq. meters	0.01	0.01	0.08	0.02	0.01	0.01

whereas the smallest (<100 sq. meters) and largest (500+ sq. meters) surface-area samples are significantly different (Table 4.35).

While changes in gross coral surface area seem to explain the increases in fish weights that occur across the complexity gradient, they do not adequately explain the differences in total species numbers and fish sizes which consistently occur between forereef and backreef zones. Differences in species (Figure 4.33C) cannot be traced to specific trophic classes or families, as large numbers of each show lower occurrence values (species per sample). They may simply be regional differences. The majority of all backreef sample sites occur in Biscayne Bay National Park (BNP) while nearly 50 percent of forereef samples occur at Molasses and Looe Key reefs. Comparisons of location-specific species tallies indicates that the latter have 10 to 15 percent more species per sample than BNP forereef sample sites which are very similar to backreef BNP sites. The consistently smaller sizes cannot be readily explained from the data. Earlier in the study it was observed that changes in morphology between zones could result in large differences in 'Scale II', surface area between sites having the same 'Scale I' or gross surface area. It may be that these consistent size differences between forereef and backreef environments are the result of finer-grained 'Scale II' morphology in backreef locations.

Fish Population Size Structure and Substrate Element Sizes

Rubble is the only bottom-cover type whose codes contain a quantitative measure of the size of its constituent elements. Three classes are distinguished in the database: large rubble (interpreted by the NMFS as basketball size and larger), small rubble and fine sand-rubble mixtures. If fish sizes respond to the geometry of elements and their interstitial spaces, then there should be evidence of size shifts in this data set. A unique size index was constructed for each rubble sample site by summing the values obtained by multiplying the proportion bottom cover in each size class by 5, 3 and 2 respectively. These numbers are used only for weighting purposes. Fish characteristics were summed and compared for four size-index subclasses.

Analysis of species and abundance characteristics by rubble size class shows the same results as in all previous sections. Median species lengths and weights increase directly with the geometric complexity of the substratum. There is an unmistakable shift to heavier and longer fish sizes in both species and abundance as the size of geometric elements in the substrata increase (Table 4.36, Figure 4.35A). This is a result of the same mechanics observed in all other analyses. The proportions of species and abundance contained in the smallest length and weight groups increase consistently as the geometric size of elements in the substratum decline while medium-sized species and fishes show proportional declines (Figures 4.35B and C). Chi-square tests suggest that there are significant differences across this gradient (Table 4.36).

These changes are not the result of shifts in trophic classes or taxonomic groups as chi-square tests show no significant differences in percentage concentrations by class across the gradient and median weights show similar trends for all classes except piscivores (Figure 4.36A). Species proportions by trophic class increase across the gradient in the smallest weight group (Figure 4.36B) and decrease in the middle (Figure 4.36C), while the largest fishes show little change (Figure 4.36D). Small and medium-sized piscivores show the same trends as other trophic classes but these are offset by gains in the largest weight group. There now seems little doubt that the size of shelter spaces plays a direct role in limiting the sizes of resident fish populations.

Table 4.36. Species and abundance characteristics and statistical tests for rubble bottom-cover types by size of their constituent elements. The rubble size index was computed by multiplying the proportion in each of 3 size classes (big rubble, small rubble and sand-rubble) by arbitrary values of 5, 3 and 2 respectively. These were summed for each sample site and index ranges established. Statistical-test values represent significant alpha levels below 0.20. NS equals 'not significant'.

Rubble Size Index	4 to 5	3 to 3.9	2.5 to 2.9	1 to 2.4
Sample Size	9	21	21	11
Mean Species Per Sample	19.8	23.2	21	15.3
Less than 10 grams	9.7	10.5	12	10.3
10 to 100 grams	5.9	7.9	6.1	3
100 to 1000 grams	3.8	4.2	2	1.5
1000 plus grams	0.4	0.6	0.8	0.5
Mean Fish Length (cm)	11.5	12.3	10.7	9.7
Median Fish Length (cm)	8.2	8.2	6.6	5.5
Proportion Species by Length Group				
1-9.9 cm	0.528	0.552	0.652	0.696
10-19.9 cm	0.331	0.265	0.223	0.196
20+ cm	0.14	0.183	0.125	0.107
Median Fish Weight (grams)	10.4	14.4	5.8	3.5
Proportion Species by Fish Weight				
Less than 10 grams	0.489	0.452	0.575	0.673
10 to 100 grams	0.298	0.341	0.291	0.196
100 to 1000 grams	0.191	0.183	0.098	0.101
1000 plus grams	0.022	0.025	0.036	0.03
Mean Abundance Per Sample	340.6	327.3	283.2	174.8
Proportion Abundance by Length Group				
1-9.9 cm	0.861	0.776	0.88	0.929
10-19.9 cm	0.119	0.185	0.092	0.051
20+ cm	0.02	0.038	0.028	0.02
Proportion Abundance by Weight Group				
Less than 10 grams	0.853	0.708	0.854	0.916
10-100 grams	0.079	0.227	0.111	0.06
100-1000 grams	0.066	0.061	0.029	0.021
1000-plus grams	0.002	0.004	0.006	0.003
Chi-square Tests: Proportion Species by Weight Group	Index = 4 to 5	Index = 3 to 3.9	Index = 2.5 to 2.9	Index = 1 to 2.4
Index = 4 to 5		NS	0.16	0.03
Index = 3 to 3.9	NS		0.11	0.01
Index = 2.5 to 2.9	0.16	0.11		NS
Index = 1 to 2.4	0.03	0.01	NS	

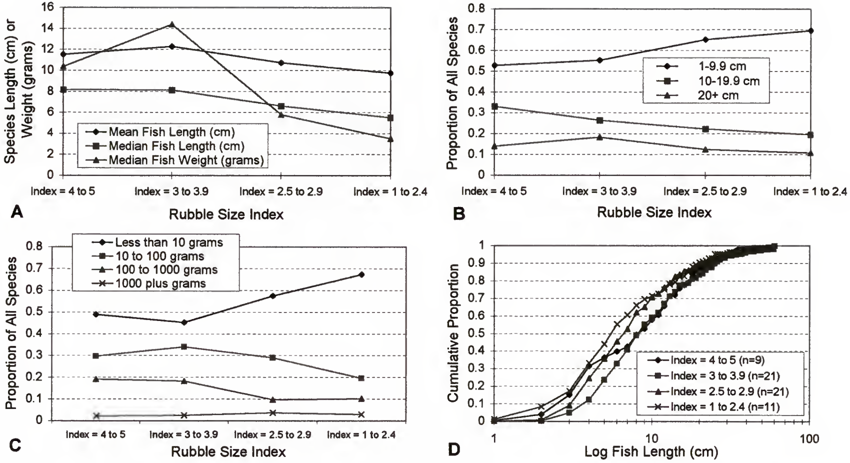

Figure 4.35. Species characteristics of rubble bottom covers by size of constituent geometric elements. The rubble size index was computed by multiplying the proportion in each of 3 size classes (big rubble, small rubble and sand-rubble) by arbitrary values of 5, 3 and 2 respectively. These were summed for each sample site and index size ranges established.
A) Mean and median fish weight and length. B) Proportion of all species by length group.
C) Proportion of all species by weight group. D) Cumulative frequency of species by fish length.

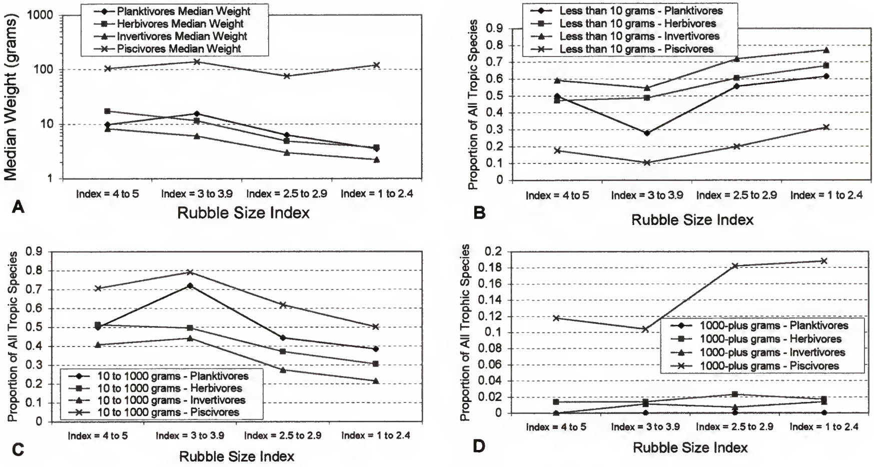

Figure 4.36. Species characteristics by trophic class for rubble bottom covers by size of constituent geometric elements. The rubble size index was computed for each sample by multiplying the proportion in each of 3 size classes (big rubble, small rubble and sand-rubble) by arbitrary values of 5, 3 and 2 respectively. Index size ranges were then established.
A) Median weight by trophic class. B) Proportion of all trophic species weighing less than 10 grams.
C) Proportion of all trophic species weighing 10 to 1000 grams. D) Proportion of all trophic species weighing 1000 or more

Forced Changes in Substrate Geometry: The Case of the M/V Wellwood

What happens to the morphological and numerical characteristics of fish populations in reefscapes whose geometric substrate characteristics have been dramatically altered by natural or human events? In 1984, the freighter M/V Wellwood ran aground on the forereef zone of Molasses Reef. Over several years, the National Marine Fisheries Service (NMFS) collected 139 fish-population samples from both the impact site and adjacent control sites. Control site bottom cover averages 55.2 percent coral, 17.6 percent rubble and 1.3 percent rock. In contrast, the impact site averages 4.8 percent coral, 48.5 percent rubble and 41.0 percent rock. For practical purposes, this grounding reduced a predominately coral reefscape to one dominated by rubble and bare rock.

Analysis indicates that fish populations in the impact site now have size and mass characteristics indistinguishable from those of homogeneous rock and rubble sample sites, whereas control-site samples more closely resemble the size characteristics of homogeneous coral bottom covers. If the geometric and biotic characteristics of the impact site were originally very similar to the control sites, then clearly the size and body-mass characteristics of their resident fish populations have changed dramatically. While the mean number of species per sample is essentially the same, mean biomass per sample declines by 50 percent and median species weights decline by 62 percent at the impact site (Table 4.37, Figure 4.37C). This is the result of an absolute loss of 40 percent of all species occurrences and 67 percent of all abundance in the larger length and weight groups (Table 4.37, Figure 4.37D). Mean abundance actually increases by 32 percent at the impact site but is concentrated in the smallest size groups (Table 4.37). Cumulative frequency curves (Figures 4.37A and B) and chi-square

Table 4.37. Species, abundance and biomass characteristics for areas damaged by the grounding of the M/V Wellwood and surrounding control sites at Molasses Reef.

	Molasses Control (All Sites)	Molasses Coral Sites	Wellwood Damage (All Sites)	Wellwood Rock	Wellwood Rubble
Sample Size	63	38	76	18	16
Mean Species Per Sample	23.8	24.1	21.2	19.2	23.6
Mean Fish Length (cm)	14.6	14.2	12.5	12.4	12.3
Median Fish Length (cm)	11.7	11.3	8.2	8.5	7.7
Proportion Species by Length					
1-9.9 cm	0.372	0.386	0.539	0.532	0.577
10-19.9 cm	0.376	0.377	0.288	0.306	0.235
20+ cm	0.253	0.237	0.173	0.162	0.188
Median Species Weight (grams)	39.6	35.6	14.6	12.2	11.3
Proportion Species by Weight					
Less than 10 grams	0.282	0.277	0.435	0.448	0.479
10 to 99.9 grams	0.414	0.432	0.373	0.364	0.333
100 to 999.9 grams	0.276	0.266	0.156	0.159	0.148
1000-plus grams	0.029	0.024	0.035	0.029	0.04
Mean Abundance Per Sample	275	283.5	359.5	337.2	343.3
Proportion Abundance by Length					
1-9.9 cm	0.496	0.486	0.875	0.902	0.804
10-19.9 cm	0.328	0.376	0.091	0.08	0.156
20+ cm	0.176	0.138	0.034	0.017	0.04
Mean Biomass Per Sample (kg)	23.2	21.1	12.7	5.4	11.5
Trophic Proportions: Species-columns 2-3, Abundance-columns 4-5.	Molasses Control	Wellwood Damage		Molasses Control	Wellwood Damage
Planktivores	0.093	0.064		0.138	0.068
Herbivores	0.406	0.44		0.345	0.554
Invertivores	0.315	0.321		0.359	0.34
Piscivores	0.139	0.117		0.14	0.033
Chi-square Tests: Proportion Species by Length Group	Molasses Control	Molasses Coral Sites	Wellwood Damage	Wellwood Rock	Wellwood Rubble
Molasses Control		NS	0.06	0.07	0.02
Molasses Coral Control	NS		0.1	0.11	0.03
Wellwood Damage	0.06	0.1		NS	NS
Wellwood Rock	0.07	0.11	NS		NS
Wellwood Rubble	0.02	0.03	NS	NS	
Chi-square Tests: Proportion Abundance by Length Group	Molasses Control	Molasses Coral Sites	Wellwood Damage	Wellwood Rock	Wellwood Rubble
Molasses Control		NS	0.01	0.01	0.01
Molasses Coral Control	NS		0.01	0.01	0.01
Wellwood Damage	0.01	0.01		NS	NS
Wellwood Rock	0.01	0.01	NS		0.14
Wellwood Rubble	0.01	0.01	NS	0.14	

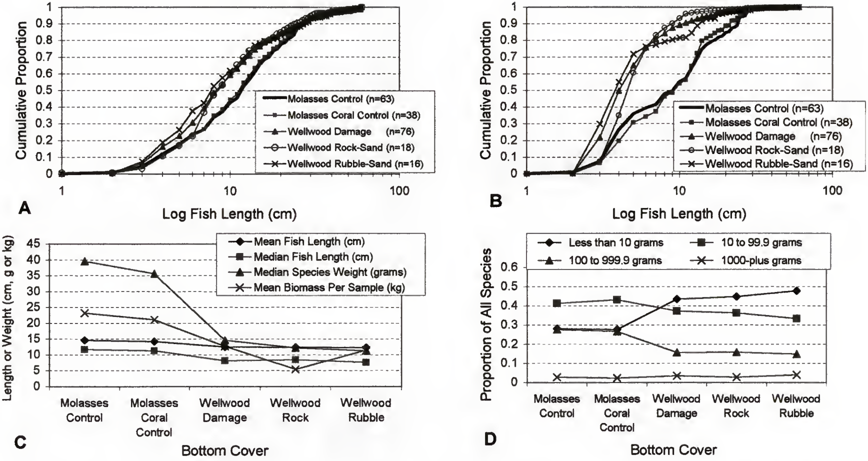

Figure 4.37. Species and abundance characteristics for areas damaged by the grounding of the M/V Wellwood and surrounding control sites at Molasses Reef. Control categories include: 1) all control sites 2) sites with 70-100 percent coral. Damage categories include: 1) all damage sites 2) homogeneous sand-rock sites 3) homogeneous sand-rubble sites. A) Cumulative frequency of species by fish length. B) Cumulative frequency of abundance by fish length. C) Lengths, weights and biomass of fish populations. D) Proportional distribution of species occurrences by weight group.

tests (Table 4.37) indicate that species and abundance size distributions are significantly different between the control and damage sites.

Assessment of the Textural-Discontinuity and Limited Shelter Hypotheses

Results from the previous sections have shown that there are significant differences in the size structure of fish populations occupying habitats composed of geometrically-different bottom-cover types. Median fish lengths and weights decline progressively from coral to rock, rubble, grass and sand substrata. These size shifts are due to decreases in the median sizes, number of occurrences and absolute abundance of species occupying the middle size groups and coincident increases in the occurrences and abundance of the smallest species. Similar size shifts have been shown to occur as total surface area decreases and as the size of constituent elements and spaces become smaller. Various researchers (Dahl, 1973; Luckhurst and Luckhurst, 1978a) have shown that surface area or geometric complexity also decreases across the same substrate types. The Textural-Discontinuity null hypothesis states that there is no significant relationship between the sizes of fishes inhabiting coral reefs and the textures of the landscapes they occupy. Given the accumulated evidence, this null hypothesis can be confidently rejected.

CHAPTER 5
CONCLUSIONS AND DISCUSSION

The distribution, abundance and diversity of fishes in coral-reef environments have been ascribed to many factors. Various authors have emphasized combinations of stochastic factors, competition, resource partitioning and predation as major forces determining the community structure of coral-reef fishes. Spatial heterogeneity has also been suggested as an important control, particularly as it relates to the availability of shelter in the face of predation (Shulman, 1984; Hixon and Beets, 1989). Certain authors have proposed a 'Limited Shelter Hypothesis' which states that appropriately-sized structural shelter is a primary control on coral-reef fish populations (Randall, 1963; Smith and Tyler, 1972, 1975; Sale and Dybdahl, 1975; Sale, 1977, 1978; Smith, 1978; Hixon and Beets, 1989). Sale (1978) notes that the majority of reef fishes appear to be limited by available living sites. Smith (1978) states that reefs appear to be crowded, with every surface and opening utilized by some organism. This hypothesis is reinforced by observations that fishes rapidly colonize artificial reefs or denuded natural reefs (Hixon and Beets, 1989; Bohnsack et al., 1994).

Many authors have noted an apparent relationship between fishes and habitat structure, particularly as they relate to shelter characteristics (Bardach, 1959; Randall, 1963; Talbot, 1965; Jones and Chase, 1975; Goldman and Talbot, 1976; Gladfelter and Gladfelter, 1978; Schulman, 1984; Hixon and Beets, 1989). A number of quantitative studies have compared fish abundance, species diversity and biomass with various measures of habitat complexity.

Species richness or diversity has been found by some authors to be correlated with substrate habitat complexity (Talbot and Goldman, 1972; Risk, 1972, Luckhurst and Luckhurst, 1978a; Molles, 1978; Talbot et al., 1978; Roberts and Ormond, 1987). Luckhurst and Luckhurst (1978a) suggested that these correlations were analogous to MacArthur's (1958) relationships between foliage height diversity and bird diversity. Fish abundance has been correlated with substrate complexity in some studies (Luckhurst and Luckhurst, 1978a; Roberts and Ormond, 1987), but not in others (Risk, 1972; Sale and Douglas, 1984). Others have found more species, individuals and body mass associated with complex branching coral forms (Hiatt and Strasburg, 1960) or more rugged structural complexes such as the spur and groove zone (Harmelin-Vivien, 1977).

Only a few studies have directly compared fish body sizes with geometric substrate properties. If the 'Limited Shelter Hypothesis' is correct, then it implies that the general size and abundance of fishes may be related to the size and numbers of structural cavities and spaces in the substratum. References to such relationships are found in the literature, but direct tests have been limited. Randall (1963) noted that reef fishes prefer hole sizes near their body size. Smith (1978) states that the sizes of openings in the reef appear to fit the size of the occupants, implying a genetic or adaptive relationship whereby fish grow to fill the size of the available spaces. Direct evidence for such relationships have been collected from both natural and artificial reef environments. Roberts and Ormond (1987) concluded that the number of substrate spaces in three size groupings accounted for 77 percent of the variance in fish abundance at some Red Sea sample sites. Luckhurst and Luckhurst (1978a) demonstrated that reef fishes greater than 50 millimeters in size, together with abundance and species diversity, were significantly correlated with their measures of gross reef morphology, the 'substrate rugosity index'. Other authors have found that the addition of very small shelter spaces associated with polypropylene rope streamers (Gorham and Alevizon, 1989) or conch shells with small, drilled holes (Shulman, 1984) significantly increased the numbers of juvenile fishes on man-made reefs. In another experiment using artificial reefs, Hixon and Beets (1989) found a direct relationship between the size of fishes recruiting to their reefs and the artificially-constructed hole sizes. They note, however, that similar studies have not been attempted on large coral reefs.

The Geometric Properties of Coral-Reef Substrata

While few quantitative studies have been conducted on the geometric characteristics of coral-reef substrata, the literature suggests that overall rugosity, or surface per unit of two-dimensional area, increases dramatically across a range of substrate types which grade from zones of small-grained detrital deposition to zones of active coral growth. There are great differences in the geometric complexity and associated surface areas of sand, grass, rubble, rock and coral substrata which are related to the physical structure or morphology of their constituent biogenic elements. Both Dahl (1973) and Luckhurst and Luckhurst (1978a) noted that surface per unit area increases as a function of horizontal and vertical extent as well as geometric form, i.e., the height and frequency of substrate elements are directly related to surface area. Mean substrate height has been shown in this study to increase directly with horizontal substrate extent, i.e., the proportion of complex bottom cover in the sample observation cylinder. Thus, the general size, range and density of geometric elements and their related interstitial spaces which provide shelter for animal populations should increase with rugosity, i.e., shelter space sizes should be directly related to the size and range of geomorphic elements that constitute the substratum across various scales.

Species Diversity, Fish Abundance and Substrate Complexity

Results of this study indicate that species diversity is directly related to general substrate complexity and surface area but not necessarily to percentage coral cover. There are statistically-significant differences in species numbers that occur between homogeneous samples of sand, grass and the more-complex bottom-cover types (coral, rock and rubble). While complex forereef structures contain significantly more species than backreef structures, there are no significant differences between coral, rock and rubble substrata within each location. Analysis of homogeneous mixtures of sand-coral, sand-rock and sand-rubble samples suggest that the mean number of species present increases directly with substrate relief and the proportion of coral, rock or rubble in the mixture. These have been shown to be directly related to gross surface area measurements, which Dahl (1973) referred to as 'gross reef morphology'. Zonal differences in larger-scale morphology may account for the consistent statistical differences in species numbers found between forereef and backreef coral locations having the same gross surface-area measurements.

These results are consistent with many other studies that have shown a positive correlation between habitat complexity (small-scale spatial heterogeneity) and species diversity in different communities. These include birds (MacArthur, 1958, 1964, 1972), rodents (Rozensweig and Winakur, 1969; M'Closkey, 1976), lizards (Pianka, 1966), insects (Murdoch et al., 1972), coral-reef gastropods (Kohn, 1967; Kohn and Leviten, 1976) and coral-reef fish populations (Talbot and Goldman, 1972; Risk, 1972; Luckhurst and Luckhurst, 1978a; Molles, 1978;

Talbot et al., 1978; Gladfelter et al., 1980; Carpenter et al., 1981; Shulman, 1984; Sano et al., 1984, 1987; Hixon and Beets, 1989; Galzin et al., 1994; Chabanet et al., 1997). They are, however, potentially at odds with those studies that have suggested that species diversity is directly related to percentage live coral cover (Carpenter et al., 1981; Sano et al., 1984, 1987; Bell and Galzin, 1984, 1988). While percentage coral cover does have a positive influence on total species present in mixed sand-coral habitats, the resulting species diversity curves are not significantly different from those occurring in sand-rubble and sand-rock environments. In fact, rubble bottom covers have consistently, if not significantly, higher numbers of species than coral substrata at all points along the sand-rubble transition.

Comparisons of mean abundance per sample show the same positive relationship to general substrate complexity and gross surface area as species diversity, except that this relationship is more linear. Fish abundance increases significantly between homogeneous sand, grass, complex-backreef and complex-forereef sample sites. No consistent statistical differences were noted between aggregate coral, rock and rubble sample sites within forereef and backreef locations. Direct, positive increases in mean abundance per sample are apparent in the transition from sand to homogeneous coral, rock and rubble bottom covers. No significant differences were noted in the slopes of the three relationships. These observations suggest that any increase in substrate complexity, regardless of type, results in a corresponding increase in the mean number of fishes and species present. The significant differences observed between complex forereef and backreef structures at all points along the transition from sand to homogeneous, complex bottom covers may be attributable to surface-area differences associated with greater relief or larger-scale changes in zonal morphology. This is consistent with the results of several studies of artificial reefs (Hixon and Beets, 1989; Bohnsack et al.,

1994) and natural reefs (Sano et al., 1984, 1987; Alcala and Gomez, 1985; Roberts and Ormond, 1987; Samoilys, 1988) that have found fish abundance to be positively correlated with the physical complexity of the substrate, particularly as it relates to shelter characteristics.

Unlike species diversity and fish abundance, coral, rock and rubble substrata show consistently different species concentrations in their faunal assemblages. These bottom-cover types share a large proportion of the species found in the regional faunal pool. Practically all of the most common species occur in each environment. Substrate-specific unique species are primarily rare and constitute a very small proportion of mean occurrences and abundance. While shared species account for more than 95 percent of all occurrences, there are great differences in species-specific relative abundance between substrate types. Species similarity indexes based on a modified version of Schoener's index of niche overlap (Gladfelter et al., 1980), indicate that similarity between samples is significantly greater within homogeneous substrate classes than between. These results compare favorably to those obtained by Gladfelter et al. (1980) in their study of faunal similarities within and between reefs having different structural characteristics. Although this study focuses on substrate types, it is noteworthy that the greatest differences in faunal similarity in their study occurred between reefs composed primarily of rubble and those containing large proportions of coral.

Within bottom-cover types, similarity rapidly increases with sample size. Individual sample sites display great variation in total species and abundance. Species composition may also vary radically since any one sample site contains only a fraction of the species in the regional pool. This results in very low similarity index values between many sites, supporting Sale's (1978) contention of randomness in the community characteristics of small areas. However, this randomness disappears with the addition of samples. Intrasubstrate differences become statistically insignificant between random samples of ten sites each.

Fish Population Size Structure and Substrate Complexity

Unlike other community characteristics, the complex bottom covers can be uniquely distinguished by the size structure of their fish populations. Median fish weights and lengths are significantly higher in coral substrata than in rock or rubble. Corals contain significantly larger proportions of species and abundance in the middle length (10-19.9 cm) and weight (10-1000 grams) groups than any other bottom-cover type. As bottom covers change to rock, rubble, grass and sand, fish concentrations shift dramatically and progressively to smaller sizes. Size structure becomes increasingly bimodal across this complexity gradient as the middle size groups decline. While fish concentrations in the smallest size groups become proportionately larger, the numbers and proportions of fishes weighing more than 1000 grams remain relatively stable.

Greater concentrations of fishes in the middle weight groups result in significantly more biomass in coral structures. Corals have two to three times the biomass of rock and rubble substrata and 200 times that of homogeneous sand bottom covers. As fishes in the middle weight groups decline, biomass becomes dramatically concentrated in the largest size groups, accounting for as much as 95 percent of all fish mass in sand bottom covers.

The fundamental mechanics of these size-structure shifts between homogeneous bottom-cover types involve three interrelated processes. Losses occur in the middle weight groups (10-100 and 100-1000 grams) due to decreases in the median weights, number of occurrences and absolute abundance of species occupying these size ranges in coral substrata. This includes the disappearance of many species in these sizes that are found only in coral bottom covers. Gains accrue to rock and rubble substrata in the smallest weight group (less than 10 grams) due to increases in the number of occurrences and absolute abundance of shared species occupying this size range. This is supplemented by an increase in the total number of species present due to weight shifts and the introduction of several species that are not found in coral bottom covers. In grass bottom covers, a large proportion of the common, shared species are very small, supporting the often-cited contention that sea grass habitats serve as nursery areas for the juveniles of many species.

Analysis of cumulative size structure within the five homogeneous bottom-cover types indicate that fish populations occupy relatively narrow size ranges whose cumulative characteristics uniquely define each substrate type. Significant differences occur between the cumulative size curves of coral substrata and all other bottom-cover types because of the large concentrations of fishes in the middle body-size ranges. As the proportions of these fishes decline, the mean cumulative frequency curves shift to significantly smaller sizes. While the bounding size curves developed from confidence intervals tend to overlap in their lower and upper ranges, it is obvious that the median fish-population size frequencies become significantly smaller as geometric bottom-cover complexity declines.

As with species and abundance, median fish lengths and weights were found to increase directly with total surface area in complex bottom covers. In homogeneous mixtures of sand and coral, these median values are directly related to the proportion of coral in the mixture, which is correlated with local relief and surface area. In sample sites having substrate relief observations, where gross, three-dimensional coral surface-area estimates could be calculated, median fish lengths and weights increased directly and significantly with surface-area values.

These variables also show a positive slope across sand-rock/rubble surface-area gradients, but are much smaller at all points along the transition than coral substrata. These increases in median species sizes do not significantly affect the cumulative size structure of fishes within specific substrate types, as fishes of all sizes show similar increases. The cumulative size curve retains its shape as its median value increases. Thus, proportional distributions of species and abundance by length and weight show few significant intrasubstrate differences across surface-area transitions.

Evaluating the Hypotheses

What factors or processes account for these differences in size structure? Four major hypotheses have been examined as causative factors in the course of this research. All represent long-standing arguments in the body of ecological literature concerning the community characteristics of coral-reef fish populations. Random processes, trophic composition, interspecific competition and geometric shelter characteristics have each been evaluated as possible mechanisms for explaining the significant size-structure differences observed in fish populations occupying homogeneous bottom covers.

None of the competing hypotheses established as alternatives to the Textural-Discontinuity and Limited Shelter Hypotheses could be shown to provide any explanation for the observed size-structure differences. In fact, tests of these alternative theses reinforced the case for the primary hypotheses. While individual sample sites do show great variability in species composition, abundance and size structure, random factors do not account for the size-structure differences observed between bottom-cover types. Random and location-specific subsamples for each bottom-cover type display cumulative size curves that do not differ significantly from the confidence-interval ranges developed for all sample sites.

While food may be an important factor in explaining the general concentrations of coral-reef fishes, changes in trophic-class concentrations between bottom-cover types do not account for the observed size-structure differences. Dahl (1973) observed that the total mass of primary producers such as algae is directly related to available surface area, while Kohn (1967) showed similar relationships for tropical gastropods. Such increases in food sources undoubtedly account for some of the positive changes in species numbers and abundance observed across surface-area gradients. Changes in the relative spatial concentrations of specific food sources such as plankton, algae and marine invertebrates very probably account for the observed changes in the proportions of planktivores, herbivores and invertivores between the five bottom-cover types. Such changes, however, cannot be linked to aggregate fish-size differences between substrate types, as mean and median trophic-class sizes are statistically similar within each bottom-cover type, and each class shows the same shift to smaller sizes across the complexity gradient.

While a large proportion of all fishes found in each bottom-cover type belong to a very small number of species, changes in these mixtures do not account for the observed size-structure differences. Dominant species found in coral, rock and rubble samples are observed in differing densities in each substrate type. Changes in their densities reflect the same mechanics as the aggregate fish populations. Small-sized coral dominants remain so in rock and rubble substrata, while mid-sized coral dominants decline significantly in size and abundance, and are replaced by smaller relatives.

The Case for the Textural-Discontinuity Hypothesis

The case for the Textural-Discontinuity Hypothesis has been made by showing that there is a direct correspondence between the size and mass of coral-reef fish populations and the geometric complexity of the substrata they occupy. Quantitative measures of fish size (length and weight) increase directly and consistently with both qualitative and quantitative measures of substrate size and complexity (substrate type, relief and surface area). The greatest differences in fish-population size structure occur between the five homogeneous bottom-cover types whose geometric differences have been established by a number of authors (Dahl, 1973; Luckhurst and Luckhurst, 1978a; Ginsburg, 1983). Within bottom-cover types, the numbers, size and mass of fishes increase directly with measures of two and three-dimensional surface area. At rubble sample sites, where crude measures of geometric element size were available, fish length and weight were shown to increase directly with this variable. Where the geometric characteristics of bottom covers are 'pulverized' into smaller geometric assemblages, such as at the grounding site of the M/V Wellwood, fish populations shift to assemblages of smaller components.

Thus, two distinct relationships are noted between the biotic and abiotic elements of the reef environment. First, the mean and median numbers of fishes and species computed across multiple sample sites increase directly with surface area. As the proportion of complex bottom cover increases, both species diversity and the number of individuals rise. The slope of this relationship is statistically similar between coral, rock and rubble substrata within each reef zone. Second, fish size increases directly with the physical complexity of the elements composing the substrata. There are significant differences between the five homogeneous bottom-cover types whose large-scale surface-area components have great geometric differences. Fish sizes also display increases across surface-area gradients within bottom-cover types. This suggests that the geometric characteristics of surfaces composed of the same type of elements may also change with scale. These relationships are shown in Figure 5.1.

These relationships show some significant differences between reef zones, which may be related to zonal differences in morphology that develop across energy gradients. Median weights, species diversity and fish abundance are significantly lower in backreef locations having the same complex bottom-cover proportions, except for rock. In rubble substrata, proportional size structure for species, abundance and biomass are statistically different between zones. This suggests that the median size of detrital elements are significantly smaller in backreef locations, since fish size has been shown to change directly with the size of constituent rubble substrate elements. Unlike rubble, the ‘hard’ bottom covers (coral and rock) show few significant differences in proportional size structure between zones, even though median species sizes are smaller in backreef environments. This suggests that coral and rock morphologies provide a more consistent range of shelter sizes than do rubble environments. Lower numbers of species and individuals in backreef locations may result from lower backreef relief, or, as noted by Dahl (1973), smaller large-scale (Scale II) surface area associated with changes in growth forms in lower-energy backreef environments. On average, these relationships appear to explain the differences in fish mass which have been observed in the course of this study.

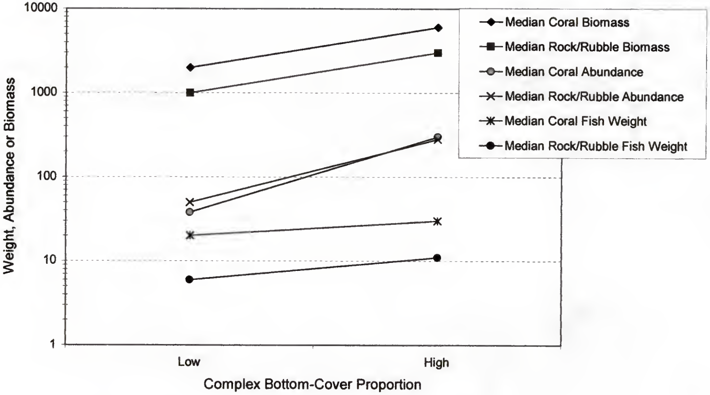

Figure 5.1. Trends in fish weight, abundance and biomass for coral and rock/rubble bottom covers across surface-area gradients.

The Case for the Limited Shelter Hypothesis

Shulman (1984) notes that spatial heterogeneity is believed to increase species diversity by providing refuges for prey. Refuges are assumed to be important because of the high levels of predation encountered in reef environments. The Limited Shelter Hypothesis states that appropriately sized structural shelter is a primary limiting resource for coral-reef fishes precisely because of such predation pressure (Hixon and Beets, 1989). Thus, the quantity of fishes in particular size ranges is limited by the availability of shelter of similar sizes. This proposition is supported by studies indicating that the numbers of juvenile fishes residing on man-made reefs can be increased by providing artificial spaces of the same general sizes (Shulman, 1984; Gorham and Alevizon, 1989; Hixon and Beets, 1989). Hixon and Beets (1989) noted a 'strong negative relationship' between the numbers of large piscivorous fishes residing on their artificial reefs and the abundance of small prey fishes.

Results of this study suggest that appropriately sized structural shelter does appear to be a primary limiting resource for reef fishes inhabiting bottom covers of different geometric complexities. Although no measures of substrate cavity sizes are available, there is an adequate theoretical and qualitative basis for stating that such refuge features decline in size across the coral-rock-rubble-grass-sand complexity gradient. Such changes have been shown throughout this study to be accompanied by similar changes in the size structure of fish populations. As total gross surface area increases in any bottom-cover type, total fish species, abundance and sizes go up. Lacking other causal mechanisms, this suggests that both total refuges and the size of those refuges increase directly with gross surface area. The physical reduction of complex, geometric reefscapes to finer-grained remnants results in smaller refuge spaces and, consequently, smaller fish populations.

Research Contributions

This research makes several contributions to the evolving body of literature dealing with the community characteristics of coral-reef fish populations. First, it clearly establishes that there is a direct, positive relationship between the size characteristics of coral-reef fish populations and the geometric characteristics of the substrata, which they occupy. Homogeneous bottom-cover types composed of coral, rock, rubble, grass and sand display fish-population size structures whose cumulative properties uniquely define each substrate type across a narrow range of sizes. These results are consistent with those of artificial-reef studies published by Hixon and Beets (1989) and the qualitative observations of other authors (Randall, 1963; Smith, 1978; Robertson and Sheldon, 1979) linking fish size to the geometry of shelter spaces. This study has made the transition called for by Hixon and Beets (1989) from their very large-scale artificial test areas to a mesoscale-sampling frame encompassing selected zones of whole reef systems.

Second, this study demonstrates that species diversity and fish abundance are directly related to gross substrate surface area. While there are large variations in these measures between individual sample sites, which must be attributable to other factors, there is a clear positive trend in these variables across surface-area gradients when viewed from a smaller-scale perspective. Such changes would be expected to result from increases in food and shelter associated with increasing surface area. These results are consistent with many other studies that have correlated species diversity with substrate complexity (Talbot and Goldman, 1972;

Risk, 1972; Luckhurst and Luckhurst, 1978a; Molles, 1978; Talbot et al., 1978; Roberts and Ormond, 1987) but only three (Luckhurst and Luckhurst, 1978a; Shulman, 1984; Roberts and Ormond, 1987) that found the same positive relationship with abundance. Inconsistencies in the latter case may be the result of differences in scale since abundance has much greater variation between sample sites.

This research provides a preliminary set of causative relationships between measured variables and processes, which, with some improvement, may be used for modeling fish characteristics and productivity in coral-reef ecosystems. McClanahan (1997) states that one of the major challenges for coral-reef ecologists is 'to develop simple assays that determine processes' in coral-reef environments, which may be incorporated into predictive models for use in monitoring and management programs. Since coral reefs support important subsistence fisheries in many areas of the world, the ability to model productivity and sustainable harvest levels with a minimum of expensive data inputs may be critical to successful management efforts. Generalized bottom cover inventories by type are relatively easy to construct in shallow, tropical water columns from aerial imagery and photographs. If the relationships established between fish-population characteristics, surface area and substrate types in the Florida Reef Tract are generally applicable to all coral-reef ecosystems, then inventories of substrate types may be used a one keystone variable in the modeling process.

Limitations and Recommendations for Further Research

Several limitations are noted for the results of this study that affects their potential utility for modeling purposes. First, fish weight and abundance, which are the primary components in biomass estimates, display great variation between individual sample sites. While random aggregations of as few as ten sample sites remove much of this variance, statistical outliers still create problems, particularly for sample categories having few observations. Second, consistent zonal differences in species diversity, abundance and fish weight between samples having similar two-dimensional surface area present another area of concern. While known differences in large-scale morphology provide a logical explanation for these phenomena, the database contains no indicator variables that may be tested.

To address these issues, research is recommended in three general areas. First, the number of sample sites used for quantifying the relationships between fish-population characteristics and substrate geometry should be expanded in several areas. In particular, there are relatively few samples available for analyzing trends in total abundance and fish sizes across sand-rock/rubble transitions. Samples for sand-coral mixtures having less than 30 percent coral bottom cover are similarly scarce.

Second, additional analyses need to be conducted to test other causative variables. These include predation, spatial proximity of different habitat types, resident and non-resident species, and the range of substrate cavity sizes by bottom-cover type in different zones. While it is not possible to evaluate fish-population size structure in the absence of predation, it is possible to analyze the effects of reduced predation pressure by comparing samples at Looe Key Reef, where predator populations were seriously reduced by years of spear fishing, to sites at Molasses and French Reefs, which were protected from spear fishing during the same time period (Bohnsack, 1982). The spatial proximity of different habitat types may affect the abundance of certain reef species that forage in surrounding habitats. Ogden (1977) found that the concentration of grunts was much higher on reefs in close proximity to sea-grass beds. Size structure and abundance may also be different between resident and non-resident species.

Such differences were noted between piscivores and other trophic classes. It is also tempting to suggest that detailed surveys of substrate cavity sizes should be conducted to more thoroughly evaluate the relationships between this variable and fish-population size structure, particularly between forereef and backreef zones. Roberts and Ormond (1987) found that the number of substrate holes in three sizes accounted for 77 percent of the variance in fish abundance at their Red Sea sample sites. However, they did not compare any measures of fish size. While such surveys might provide valuable information, the number of samples required would likely be large and the costs prohibitive.

Third, the causative relationships established in this study for homogeneous sample sites should be extended to the multitude of heterogeneous sites that constitute the majority of all samples. Do mixtures of coral, rock and rubble have intermediate fish-population size structures and biomass, or are they more similar to coral substrata? The algorithms should be incorporated into a simple predictive model, where proportion bottom cover by type and reef location are the primary independent variables. Such a model could be initially tested against aggregations of sample sites in the NMFS database. Fish-population size and mass characteristics for specific bottom-cover types may be predicted for aggregate sample sites from two related independent variables and their associated process rates. Proportion complex bottom cover is the first independent variable and is a proxy for Dahl's (1973) measure of Scale I surface area, or gross reef morphology, which is associated with overall structure size. Results of this study suggest that fish weight, abundance and biomass increase directly with this surface-area measure (Figure 5.1). Bottom-cover type and location is the second independent variable and is a proxy for Dahl's (1973) measure of Scale II surface area, which is associated with larger-scale surface features such as coral colonies, branches and detrital materials. Study results indicate that fish size varies directly and significantly with these measures, thus affecting overall biomass (Figure 5.1). It is suspected that these features become larger as Scale I surface area increases, thus accounting for fish-size increases which are observed across Scale I surface-area gradients (Figure 5.1).

The spatial model depicted in Figure 5.2 is simplistic and does not account for the multiple feedback loops and additional variables that would likely be necessary in a final model. It is presented here merely as an example of how the relationships developed in this research might be applied to developing a low-cost, reef-fish productivity model. Bottom-cover classification would be conducted based on imagery, aerial photography and ground surveys. A sample grid would then be superimposed on these substrate surfaces and bottom-cover areas calculated. The size of each grid should be related to an important variable, such as the size of the sample observation cylinder in the case of the NMFS database, or the home range of the largest reef-related piscivore species. Total biomass estimates would then be developed based on predictions of fish abundance by bottom-cover mixture allocated to fish length and weight.

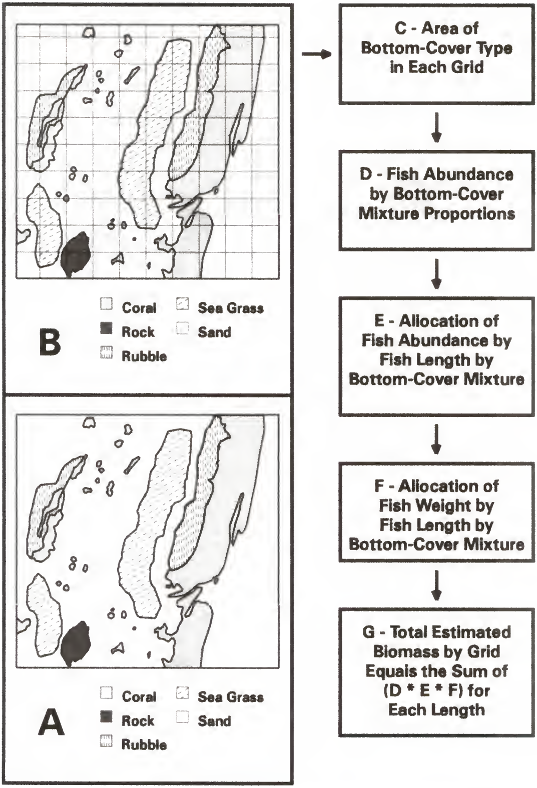
C - Area of Bottom-Cover Type in Each Grid
D - Fish Abundance by Bottom-Cover Mixture Proportions
E - Allocation of Fish Abundance by Fish Length by Bottom-Cover Mixture
F - Allocation of Fish Weight by Fish Length by Bottom-Cover Mixture
G - Total Estimated Biomass by Grid Equals the Sum of (D * E * F) for Each Length
B
Coral
Sea Grass
Rock
Sand
Rubble
A
Coral
Sea Grass
Rock
Sand
Rubble

Figure 5.2. Main Components of a Simplistic Model for Estimating Fish Biomass in Coral-Reef Ecosystems. A) Substrate Classification from Imagery, Aerial Photography and/or Ground Surveys. B) Substrate Classification with Superimposed Sample Grid. C-G) Biomass Calculation Submodules.

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APPENDIX A

DESCRIPTIVE STATISTICS FOR SPECIES AND ABUNDANCE IN MIXED, SAND-CORAL AND SAND-ROCK/RUBBLE SUBSTRATA

Table A.1. Descriptive statistics for species in mixed, sand-coral substrata by percent coral in the mixture.

Percent Coral Bottom Cover	0	5-19	20-29	30-39	40-49	50-59	60-69	70-79	80-89	90-99	100
Sample Size	16	2	7	10	27	70	76	93	85	105	135
Mean Species Per Sample	2.1	9.5	14.7	15.7	18.7	18.8	20.9	20.7	21.9	21.0	20.8
Standard Deviation	1.1	0.7	6.5	5.5	5.2	5.6	5.1	5.4	4.9	5.3	5.3
Sample Variance	1.3	0.5	42.6	30.2	26.7	30.8	25.8	29.1	24.5	27.8	28.1
0.05 Confidence Interval	0.6	1	4.8	3.4	1.9	1.3	1.1	1.1	1.1	1.0	0.9
Lower 0.05 Confidence Bound	1.6	0	9.9	12.3	16.8	17.5	19.8	19.6	20.9	19.9	19.9
Upper 0.05 Confidence Bound	2.7	10.5	19.5	19.1	20.7	20.1	22.1	21.8	23.0	22.0	21.7
Minimum Value	1.0	9.0	6.0	4.0	8.0	2.0	8.0	2.0	10.0	10.0	7.0
First Quartile	1.0	9.3	10.0	13.5	17.0	15.0	17.0	17.0	18.0	17.0	17.0
Second Quartile (median)	2.0	9.5	15.0	16.5	19.0	19.5	22.0	21.0	23.0	21.0	21.0
Third Quartile	3.0	9.8	20.0	18.8	22.0	22.0	24.0	24.0	25.0	25.0	24.0
Maximum Value	4.0	10.0	22.0	24.0	28.0	31.0	32.0	32.0	33.0	34.0	34.0

Table A.2. Descriptive statistics for abundance in mixed, sand-coral substrata by percent coral in the mixture.

Percent Coral Bottom Cover	0	5-19	20-29	30-39	40-49	50-59
Sample Size	16	2	7	10	27	70
Mean Abundance Per Sample	19.4	37.5	213.4	106.7	160.5	142.6
Standard Deviation	22.8	27.6	224.4	46.7	147.0	101.8
Sample Variance	519.9	760.5	50373.3	2177.6	21607.5	10371.2
0.05 Confidence Interval	11.2	38.2	166.3	28.9	55.4	23.9
Lower 0.05 Confidence Bound	8.3	0.0	47.2	77.8	105.0	118.8
Upper 0.05 Confidence Bound	30.6	75.7	379.7	135.6	215.9	166.5
Minimum Value	1.0	18.0	50.0	38.0	25.0	3.0
First Quartile	4.0	27.8	52.5	74.3	77.5	82.3
Second Quartile (median)	11.5	37.5	123.0	96.5	109.0	108.5
Third Quartile	24.3	47.3	288.0	137.8	197.5	186.5
Maximum Value	80.0	57.0	640.0	180.0	707.0	495.0

Percent Coral Bottom Cover	60-69	70-79	80-89	90-99	100
Sample Size	76	93	85	105	135
Mean Abundance Per Sample	199.4	173.1	228.2	201.7	275.2
Standard Deviation	137.0	130.7	144.8	128.7	213.5
Sample Variance	18757.5	17090.3	20978.8	16562.4	45580.2
0.05 Confidence Interval	30.8	26.6	30.8	24.6	36.0
Lower 0.05 Confidence Bound	168.6	146.5	197.4	177.1	239.2
Upper 0.05 Confidence Bound	230.2	199.7	259.0	226.3	311.2
Minimum Value	36.0	6.0	39.0	33.0	16.0
First Quartile	108.5	93.0	113.0	106.0	130.0
Second Quartile (median)	149.5	129.0	190.0	177.0	222.0
Third Quartile	260.3	215.0	326.0	280.0	361.5
Maximum Value	667.0	773.0	601.0	708.0	1260.0

Table A.3. Descriptive statistics for species and abundance in mixed, sand-rock/rubble substrata by percent rock and rubble in the mixture

Percent Rock/Rubble Bottom Cover	5-29	30-49	50-69	70-89	90-99	100
Sample Size	8	3	8	20	33	63
Mean Species Per Sample	13.3	21.0	18.9	19.5	21.0	19.6
Standard Deviation	6.7	2.6	5.0	4.5	4.9	4.4
Sample Variance	44.5	7.0	24.7	20.7	24.0	19.0
0.05 Confidence Interval	4.6	3.0	3.4	2.0	1.7	1.1
Lower 0.05 Confidence Bound	8.6	0.0	15.4	17.5	19.3	18.5
Upper 0.05 Confidence Bound	17.9	24.0	22.3	21.5	22.6	20.6
Minimum Value	6.0	18.0	13.0	10.0	6.0	10.0
First Quartile	9.0	20.0	14.5	15.8	19.0	16.0
Second Quartile (median)	11.5	22.0	19.0	20.5	22.0	20.0
Third Quartile	15.0	22.5	23.3	21.0	24.0	23.0
Maximum Value	27.0	23.0	25.0	30.0	29.0	27.0
Percent Rock/Rubble Bottom Cover	5-29	30-49	50-69	70-89	90-99	100
Sample Size	8	3	8	20	33	63
Mean Abundance Per Sample	82.1	202.7	267.1	207.2	303.5	278.4
Standard Deviation	82.2	147.1	192.1	120.3	177.9	158.5
Sample Variance	6760.4	21636.3	36903.6	14462.9	31640.4	25126.9
0.05 Confidence Interval	57.0	166.4	133.1	52.7	60.7	39.1
Lower 0.05 Confidence Bound	25.1	0.0	134.0	154.5	242.9	239.3
Upper 0.05 Confidence Bound	139.1	369.1	400.2	259.9	364.2	317.6
Minimum Value	25.0	67.0	39.0	90.0	13.0	50.0
First Quartile	36.5	124.5	123.0	123.3	170.0	137.5
Second Quartile (median)	47.0	182.0	238.0	162.0	301.0	266.0
Third Quartile	81.8	270.5	377.3	244.8	411.0	373.5
Maximum Value	267.0	359.0	569.0	517.0	817.0	766.0

APPENDIX B
CUMULATIVE PROPERTIES OF SPECIES, ABUNDANCE AND BIOMASS BY FISH LENGTH FOR HOMOGENEOUS SUBSTRATE TYPES

Table B.1. Cumulative proportion of species by fish length for homogeneous coral bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound	Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.001	0.010	31	0.913	0.945	0.976
2	0.000	0.008	0.027	32	0.915	0.949	0.980
3	0.006	0.038	0.078	33	0.923	0.953	0.981
4	0.029	0.093	0.159	34	0.925	0.954	0.981
5	0.087	0.164	0.265	35	0.938	0.965	0.991
6	0.121	0.219	0.342	36	0.940	0.967	0.991
7	0.168	0.281	0.408	37	0.942	0.969	0.991
8	0.241	0.354	0.486	38	0.945	0.973	0.993
9	0.273	0.395	0.552	39	0.946	0.974	0.993
10	0.305	0.449	0.634	40	0.957	0.981	0.995
11	0.358	0.499	0.673	41	0.960	0.981	0.995
12	0.411	0.559	0.732	42	0.962	0.982	0.995
13	0.470	0.606	0.770	43	0.964	0.983	0.995
14	0.511	0.642	0.789	44	0.964	0.983	0.995
15	0.573	0.687	0.819	45	0.970	0.988	0.999
16	0.600	0.708	0.838	46	0.972	0.988	0.999
17	0.627	0.730	0.849	47	0.973	0.988	0.999
18	0.675	0.761	0.865	48	0.973	0.988	0.999
19	0.695	0.779	0.872	49	0.973	0.988	0.999
20	0.727	0.810	0.902	50	0.974	0.990	1.000
21	0.735	0.818	0.902	51	0.976	0.991	1.000
22	0.752	0.835	0.916	52	0.976	0.991	1.000
23	0.783	0.853	0.922	53	0.978	0.991	1.000
24	0.804	0.864	0.923	54	0.978	0.991	1.000
25	0.841	0.893	0.945	55	0.981	0.992	1.000
26	0.848	0.896	0.945	56	0.981	0.992	1.000
27	0.857	0.903	0.947	57	0.981	0.992	1.000
28	0.876	0.916	0.952	58	0.982	0.992	1.000
29	0.890	0.921	0.952	59	0.982	0.992	1.000
30	0.910	0.942	0.976	60	1.000	1.000	1.000

Table B.2. Cumulative proportion of species by fish length for homogeneous rock bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound	Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.003	0.008	31	0.909	0.942	0.971
2	0.000	0.012	0.071	32	0.909	0.947	0.978
3	0.009	0.043	0.164	33	0.909	0.952	0.979
4	0.070	0.120	0.271	34	0.909	0.954	0.979
5	0.131	0.185	0.338	35	0.912	0.954	0.981
6	0.194	0.255	0.446	36	0.912	0.956	0.981
7	0.306	0.388	0.559	37	0.912	0.956	0.981
8	0.408	0.491	0.653	38	0.912	0.959	0.982
9	0.461	0.544	0.688	39	0.912	0.961	0.985
10	0.519	0.598	0.698	40	0.912	0.966	0.988
11	0.561	0.639	0.725	41	0.912	0.966	0.988
12	0.611	0.680	0.759	42	0.912	0.969	0.988
13	0.648	0.713	0.790	43	0.914	0.969	0.988
14	0.673	0.740	0.822	44	0.914	0.969	0.988
15	0.704	0.759	0.836	45	0.918	0.971	0.990
16	0.738	0.779	0.853	46	0.918	0.971	0.990
17	0.755	0.795	0.863	47	0.918	0.973	0.991
18	0.774	0.809	0.876	48	0.918	0.974	0.992
19	0.784	0.831	0.897	49	0.918	0.974	0.992
20	0.806	0.846	0.917	50	0.937	0.981	1.000
21	0.809	0.858	0.921	51	0.937	0.981	1.000
22	0.827	0.868	0.940	52	0.937	0.981	1.000
23	0.843	0.880	0.953	53	0.937	0.985	1.000
24	0.848	0.889	0.953	54	0.937	0.985	1.000
25	0.866	0.901	0.958	55	0.937	0.986	1.000
26	0.869	0.903	0.961	56	0.937	0.986	1.000
27	0.869	0.911	0.961	57	0.937	0.988	1.000
28	0.878	0.923	0.968	58	0.937	0.991	1.000
29	0.883	0.925	0.970	59	0.937	0.991	1.000
30	0.909	0.935	0.971	60	1.000	1.000	1.000

Table B.3. Cumulative proportion of species by fish length for homogeneous rubble bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound	Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.002	0.007	31	0.922	0.944	0.985
2	0.000	0.011	0.028	32	0.924	0.946	0.985
3	0.021	0.081	0.120	33	0.933	0.953	0.990
4	0.096	0.197	0.322	34	0.935	0.954	0.990
5	0.216	0.293	0.498	35	0.940	0.958	0.990
6	0.287	0.380	0.610	36	0.944	0.960	0.990
7	0.357	0.455	0.719	37	0.945	0.962	0.994
8	0.454	0.544	0.761	38	0.955	0.968	0.994
9	0.506	0.590	0.804	39	0.955	0.968	0.994
10	0.557	0.637	0.833	40	0.963	0.973	0.994
11	0.583	0.662	0.845	41	0.964	0.974	0.994
12	0.632	0.702	0.863	42	0.966	0.975	0.994
13	0.681	0.743	0.878	43	0.966	0.976	0.994
14	0.712	0.770	0.887	44	0.966	0.977	0.994
15	0.741	0.792	0.902	45	0.966	0.982	0.994
16	0.757	0.805	0.906	46	0.966	0.982	0.994
17	0.765	0.812	0.911	47	0.966	0.982	0.994
18	0.788	0.833	0.929	48	0.966	0.982	0.994
19	0.789	0.838	0.949	49	0.966	0.982	0.994
20	0.808	0.856	0.952	50	0.966	0.984	0.994
21	0.815	0.863	0.954	51	0.966	0.984	0.994
22	0.829	0.875	0.960	52	0.966	0.984	0.994
23	0.844	0.888	0.970	53	0.966	0.985	0.995
24	0.850	0.892	0.970	54	0.966	0.985	0.995
25	0.867	0.905	0.978	55	0.966	0.989	0.999
26	0.872	0.911	0.981	56	0.966	0.989	0.999
27	0.882	0.918	0.981	57	0.966	0.989	0.999
28	0.893	0.924	0.981	58	0.966	0.989	0.999
29	0.901	0.930	0.985	59	0.966	0.989	0.999
30	0.920	0.943	0.985	60	1.000	1.000	1.000

Table B.4. Cumulative proportion of species by fish length for homogeneous grass bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound	Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.010	0.026	31	0.915	0.929	0.975
2	0.002	0.033	0.057	32	0.918	0.933	0.977
3	0.082	0.143	0.192	33	0.918	0.933	0.977
4	0.284	0.348	0.464	34	0.925	0.938	0.976
5	0.404	0.486	0.609	35	0.925	0.938	0.976
6	0.535	0.595	0.721	36	0.925	0.938	0.976
7	0.596	0.633	0.770	37	0.925	0.938	0.976
8	0.645	0.681	0.814	38	0.928	0.943	0.979
9	0.683	0.719	0.844	39	0.928	0.943	0.979
10	0.706	0.738	0.855	40	0.932	0.952	0.983
11	0.722	0.752	0.869	41	0.932	0.952	0.983
12	0.723	0.757	0.870	42	0.932	0.952	0.983
13	0.725	0.762	0.871	43	0.932	0.952	0.983
14	0.729	0.767	0.877	44	0.932	0.952	0.983
15	0.739	0.781	0.885	45	0.938	0.957	0.984
16	0.755	0.795	0.896	46	0.938	0.957	0.984
17	0.755	0.795	0.896	47	0.938	0.957	0.984
18	0.762	0.810	0.902	48	0.938	0.957	0.984
19	0.770	0.819	0.906	49	0.938	0.957	0.984
20	0.793	0.838	0.924	50	0.938	0.957	0.984
21	0.799	0.843	0.930	51	0.938	0.957	0.984
22	0.800	0.848	0.931	52	0.938	0.957	0.984
23	0.803	0.852	0.933	53	0.938	0.957	0.984
24	0.833	0.867	0.943	54	0.938	0.957	0.984
25	0.850	0.890	0.955	55	0.938	0.957	0.984
26	0.871	0.905	0.955	56	0.938	0.957	0.984
27	0.871	0.905	0.955	57	0.938	0.957	0.984
28	0.877	0.910	0.955	58	0.938	0.957	0.984
29	0.877	0.910	0.955	59	0.938	0.957	0.984
30	0.915	0.929	0.975	60	1.000	1.000	1.000

Table B.5. Cumulative proportion of species by fish length for homogeneous sand bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.059	0.198
2	0.000	0.118	0.239
3	0.031	0.176	0.292
4	0.056	0.265	0.392
5	0.332	0.529	0.699
6	0.524	0.676	0.862
7	0.547	0.706	0.870
8	0.577	0.765	0.913
9	0.595	0.794	0.936
10	0.628	0.853	0.966
11	0.628	0.853	0.966
12	0.628	0.853	0.966
13	0.628	0.853	0.966
14	0.628	0.853	0.966
15	0.628	0.853	0.966
16	0.662	0.882	0.994
17	0.662	0.882	0.994
18	0.662	0.882	0.994
19	0.662	0.882	0.994
20	0.761	0.912	1.000
21	0.761	0.912	1.000
22	0.761	0.912	1.000
23	0.889	0.941	1.000
24	0.889	0.941	1.000
25	0.889	0.941	1.000
26	0.889	0.941	1.000
27	0.889	0.941	1.000
28	0.889	0.941	1.000
29	0.889	0.941	1.000
30	0.889	0.941	1.000
31	0.889	0.941	1.000
32	0.889	0.941	1.000
33	0.889	0.941	1.000
34	0.889	0.941	1.000
35	0.889	0.941	1.000
36	0.889	0.941	1.000
37	0.889	0.941	1.000
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41	0.889	0.941	1.000
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43	0.889	0.941	1.000
44	0.889	0.941	1.000
45	0.889	0.941	1.000
46	0.889	0.941	1.000
47	0.889	0.941	1.000
48	0.889	0.941	1.000
49	0.889	0.941	1.000
50	0.889	0.941	1.000
51	0.889	0.941	1.000
52	0.889	0.941	1.000
53	0.889	0.941	1.000
54	0.889	0.941	1.000
55	0.889	0.941	1.000
56	0.889	0.941	1.000
57	0.889	0.941	1.000
58	0.889	0.941	1.000
59	0.889	0.941	1.000
60	1.000	1.000	1.000

Table B.6. Cumulative proportion of abundance by fish length for homogeneous coral bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.000	0.001
2	0.000	0.008	0.070
3	0.006	0.142	0.152
4	0.054	0.292	0.379
5	0.194	0.445	0.588
6	0.279	0.504	0.648
7	0.306	0.539	0.679
8	0.369	0.586	0.720
9	0.384	0.608	0.738
10	0.400	0.637	0.782
11	0.454	0.685	0.819
12	0.516	0.736	0.878
13	0.572	0.764	0.890
14	0.646	0.818	0.900
15	0.709	0.857	0.936
16	0.720	0.878	0.957
17	0.744	0.888	0.961
18	0.773	0.904	0.968
19	0.796	0.911	0.970
20	0.828	0.928	0.977
21	0.831	0.931	0.979
22	0.838	0.936	0.982
23	0.876	0.950	0.986
24	0.889	0.961	0.988
25	0.925	0.976	0.991
26	0.926	0.976	0.991
27	0.929	0.978	0.991
28	0.934	0.981	0.994
29	0.937	0.982	0.994
30	0.950	0.986	1.000
31	0.984	0.994	0.996
32	0.984	0.994	0.997
33	0.985	0.995	0.997
34	0.986	0.995	0.997
35	0.987	0.996	0.998
36	0.988	0.996	0.998
37	0.988	0.996	0.998
38	0.988	0.997	0.999
39	0.988	0.997	0.999
40	0.991	0.998	0.999
41	0.992	0.998	0.999
42	0.992	0.998	0.999
43	0.992	0.998	0.999
44	0.992	0.998	0.999
45	0.994	0.999	1.000
46	0.995	0.999	1.000
47	0.995	0.999	1.000
48	0.995	0.999	1.000
49	0.995	0.999	1.000
50	0.995	0.999	1.000
51	0.996	0.999	1.000
52	0.996	0.999	1.000
53	0.996	0.999	1.000
54	0.996	0.999	1.000
55	0.996	0.999	1.000
56	0.996	0.999	1.000
57	0.996	0.999	1.000
58	0.996	0.999	1.000
59	0.996	0.999	1.000
60	1.000	1.000	1.000

Table B.7. Cumulative proportion of abundance by fish length for homogeneous rock bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.001	0.002
2	0.000	0.020	0.203
3	0.040	0.085	0.308
4	0.125	0.314	0.363
5	0.203	0.535	0.575
6	0.384	0.670	0.695
7	0.491	0.749	0.775
8	0.540	0.793	0.828
9	0.570	0.818	0.856
10	0.633	0.856	0.883
11	0.644	0.880	0.912
12	0.670	0.891	0.933
13	0.689	0.897	0.948
14	0.696	0.901	0.965
15	0.703	0.904	0.973
16	0.725	0.916	0.989
17	0.737	0.918	0.994
18	0.739	0.921	1.000
19	0.784	0.937	1.000
20	0.864	0.940	1.000
21	0.867	0.941	1.000
22	0.879	0.942	1.000
23	0.888	0.944	1.000
24	0.888	0.945	1.000
25	0.891	0.949	1.000
26	0.892	0.949	1.000
27	0.892	0.953	1.000
28	0.900	0.954	1.000
29	0.900	0.955	1.000
30	0.908	0.956	1.000
31	0.908	0.956	1.000
32	0.908	0.994	1.000
33	0.908	0.994	1.000
34	0.908	0.994	1.000
35	0.909	0.994	1.000
36	0.909	0.995	1.000
37	0.909	0.995	1.000
38	0.909	0.995	1.000
39	0.909	0.995	1.000
40	0.909	0.996	1.000
41	0.909	0.996	1.000
42	0.909	0.996	1.000
43	0.909	0.996	1.000
44	0.909	0.996	1.000
45	0.910	0.996	1.000
46	0.910	0.996	1.000
47	0.910	0.996	1.000
48	0.910	0.996	1.000
49	0.910	0.996	1.000
50	0.913	0.997	1.000
51	0.913	0.997	1.000
52	0.913	0.997	1.000
53	0.913	0.998	1.000
54	0.913	0.998	1.000
55	0.913	0.998	1.000
56	0.913	0.998	1.000
57	0.913	0.998	1.000
58	0.913	0.999	1.000
59	0.913	0.999	1.000
60	1.000	1.000	1.000

Table B.8. Cumulative proportion of abundance by fish length for homogeneous rubble bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound	Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.000	0.001	31	0.985	0.993	0.998
2	0.000	0.058	0.113	32	0.985	0.993	0.998
3	0.015	0.268	0.434	33	0.985	0.993	0.999
4	0.185	0.594	0.745	34	0.986	0.994	0.999
5	0.429	0.752	0.819	35	0.989	0.995	0.999
6	0.599	0.801	0.844	36	0.989	0.995	0.999
7	0.683	0.826	0.879	37	0.991	0.995	0.999
8	0.742	0.849	0.912	38	0.993	0.996	0.999
9	0.762	0.860	0.929	39	0.993	0.996	0.999
10	0.819	0.870	0.937	40	0.993	0.997	0.999
11	0.823	0.878	0.954	41	0.993	0.997	0.999
12	0.851	0.895	0.958	42	0.993	0.997	0.999
13	0.873	0.916	0.965	43	0.993	0.997	0.999
14	0.881	0.928	0.972	44	0.993	0.997	0.999
15	0.899	0.946	0.972	45	0.993	0.998	0.999
16	0.901	0.951	0.976	46	0.993	0.998	0.999
17	0.902	0.952	0.978	47	0.993	0.998	0.999
18	0.918	0.969	0.990	48	0.993	0.998	0.999
19	0.920	0.970	0.992	49	0.993	0.998	0.999
20	0.959	0.975	0.993	50	0.993	0.998	1.000
21	0.961	0.977	0.993	51	0.993	0.998	1.000
22	0.963	0.979	0.995	52	0.993	0.998	1.000
23	0.968	0.982	0.995	53	0.993	0.998	1.000
24	0.968	0.983	0.995	54	0.993	0.998	1.000
25	0.971	0.984	0.996	55	0.993	0.998	1.000
26	0.971	0.985	0.997	56	0.993	0.998	1.000
27	0.973	0.986	0.997	57	0.993	0.998	1.000
28	0.974	0.987	0.997	58	0.993	0.998	1.000
29	0.976	0.988	0.998	59	0.993	0.998	1.000
30	0.9850	0.993	0.998	60	1.000	1.000	1.000

Table B.9. Cumulative proportion of abundance by fish length for homogeneous grass bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound	Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.037	0.069	31	0.980	0.990	0.995
2	0.002	0.106	0.129	32	0.981	0.991	0.995
3	0.094	0.186	0.269	33	0.981	0.991	0.995
4	0.351	0.362	0.597	34	0.983	0.992	0.996
5	0.483	0.448	0.724	35	0.983	0.992	0.996
6	0.603	0.553	0.810	36	0.983	0.992	0.996
7	0.660	0.576	0.853	37	0.983	0.992	0.996
8	0.715	0.693	0.893	38	0.983	0.993	0.996
9	0.760	0.728	0.926	39	0.983	0.993	0.996
10	0.762	0.731	0.929	40	0.984	0.994	0.997
11	0.769	0.734	0.936	41	0.984	0.994	0.997
12	0.770	0.735	0.936	42	0.984	0.994	0.997
13	0.770	0.735	0.937	43	0.984	0.994	0.997
14	0.788	0.772	0.949	44	0.984	0.994	0.997
15	0.792	0.775	0.953	45	0.985	0.994	0.997
16	0.796	0.777	0.958	46	0.985	0.994	0.997
17	0.796	0.777	0.958	47	0.985	0.994	0.997
18	0.799	0.780	0.960	48	0.985	0.994	0.997
19	0.800	0.781	0.961	49	0.985	0.994	0.997
20	0.807	0.786	0.968	50	0.985	0.994	0.997
21	0.808	0.787	0.969	51	0.985	0.994	0.997
22	0.809	0.788	0.970	52	0.985	0.994	0.997
23	0.811	0.791	0.972	53	0.985	0.994	0.997
24	0.844	0.808	0.982	54	0.985	0.994	0.997
25	0.849	0.812	0.987	55	0.985	0.994	0.997
26	0.856	0.819	0.992	56	0.985	0.994	0.997
27	0.856	0.819	0.992	57	0.985	0.994	0.997
28	0.857	0.820	0.993	58	0.985	0.994	0.997
29	0.857	0.820	0.993	59	0.985	0.994	0.997
30	0.980	0.990	0.995	60	1.000	1.000	1.000

Table B.10. Cumulative proportion of abundance by fish length for homogeneous sand bottom covers: mean, upper and lower 95-percent confidence interval bounds.

Length (cm)	Upper Bound	Mean	Lower Bound
1	0.000	0.051	0.158
2	0.023	0.193	0.252
3	0.044	0.199	0.272
4	0.100	0.228	0.373
5	0.406	0.466	0.714
6	0.598	0.907	0.870
7	0.600	0.913	0.872
8	0.648	0.939	0.923
9	0.663	0.942	0.939
10	0.677	0.961	0.958
11	0.677	0.961	0.958
12	0.677	0.961	0.958
13	0.677	0.961	0.958
14	0.677	0.961	0.958
15	0.677	0.961	0.958
16	0.750	0.987	0.996
17	0.750	0.987	0.996
18	0.750	0.987	0.996
19	0.750	0.987	0.996
20	0.845	0.990	1.000
21	0.845	0.990	1.000
22	0.845	0.990	1.000
23	0.996	0.994	1.000
24	0.996	0.994	1.000
25	0.996	0.994	1.000
26	0.996	0.994	1.000
27	0.996	0.994	1.000
28	0.996	0.994	1.000
29	0.996	0.994	1.000
30	0.996	0.994	1.000
31	0.996	0.994	1.000
32	0.996	0.994	1.000
33	0.996	0.994	1.000
34	0.996	0.994	1.000
35	0.996	0.994	1.000
36	0.996	0.994	1.000
37	0.996	0.994	1.000
38	0.996	0.994	1.000
39	0.996	0.994	1.000
40	0.996	0.994	1.000
41	0.996	0.994	1.000
42	0.996	0.994	1.000
43	0.996	0.994	1.000
44	0.996	0.994	1.000
45	0.996	0.994	1.000
46	0.996	0.994	1.000
47	0.996	0.994	1.000
48	0.996	0.994	1.000
49	0.996	0.994	1.000
50	0.996	0.994	1.000
51	0.996	0.994	1.000
52	0.996	0.994	1.000
53	0.996	0.994	1.000
54	0.996	0.994	1.000
55	0.996	0.994	1.000
56	0.996	0.994	1.000
57	0.996	0.994	1.000
58	0.996	0.994	1.000
59	0.996	0.994	1.000
60	1.000	1.000	1.000

Table B.11. Cumulative proportion of mean biomass by fish length for homogeneous coral, rock and rubble bottom covers.

Length (cm)	All Coral (n=135)	All Rock (n=31)	All Rubble (n=41)
1	0.000	0.000	0.000
2	0.000	0.000	0.000
3	0.001	0.001	0.003
4	0.004	0.010	0.013
5	0.008	0.021	0.026
6	0.012	0.031	0.031
7	0.017	0.045	0.036
8	0.028	0.057	0.043
9	0.037	0.068	0.048
10	0.051	0.090	0.053
11	0.082	0.113	0.059
12	0.126	0.127	0.111
13	0.169	0.136	0.130
14	0.245	0.143	0.141
15	0.292	0.148	0.198
16	0.321	0.174	0.207
17	0.337	0.181	0.213
18	0.367	0.189	0.264
19	0.375	0.249	0.273
20	0.420	0.263	0.294
21	0.429	0.270	0.299
22	0.446	0.276	0.309
23	0.503	0.289	0.334
24	0.558	0.294	0.340
25	0.634	0.320	0.360
26	0.636	0.322	0.371
27	0.647	0.358	0.378
28	0.670	0.375	0.401
29	0.678	0.377	0.407
30	0.718	0.396	0.463
31	0.784	0.408	0.465
32	0.788	0.608	0.467
33	0.795	0.616	0.475
34	0.795	0.621	0.481
35	0.810	0.621	0.506
36	0.812	0.630	0.510
37	0.819	0.630	0.516
38	0.826	0.637	0.555
39	0.828	0.647	0.555
40	0.849	0.656	0.566
41	0.851	0.656	0.566
42	0.852	0.667	0.567
43	0.853	0.667	0.572
44	0.853	0.667	0.575
45	0.862	0.670	0.584
46	0.868	0.670	0.584
47	0.869	0.674	0.584
48	0.869	0.689	0.588
49	0.869	0.689	0.588
50	0.871	0.708	0.599
51	0.875	0.708	0.599
52	0.875	0.708	0.599
53	0.877	0.727	0.600
54	0.877	0.727	0.600
55	0.879	0.739	0.611
56	0.879	0.739	0.611
57	0.879	0.758	0.611
58	0.880	0.777	0.611
59	0.880	0.777	0.611
60	1.000	1.000	1.000

Table B.12. Cumulative proportion of mean biomass by fish length for homogeneous grass and sand bottom covers.

Length (cm)	Grass (n=41)	Sand (n=21)
1	0.000	0.000
2	0.000	0.001
3	0.001	0.001
4	0.003	0.001
5	0.005	0.004
6	0.009	0.014
7	0.011	0.014
8	0.031	0.016
9	0.038	0.016
10	0.039	0.020
11	0.039	0.020
12	0.040	0.020
13	0.040	0.020
14	0.078	0.020
15	0.080	0.020
16	0.082	0.042
17	0.082	0.042
18	0.087	0.042
19	0.090	0.042
20	0.102	0.045
21	0.103	0.045
22	0.107	0.045
23	0.115	0.055
24	0.174	0.055
25	0.192	0.055
26	0.222	0.055
27	0.222	0.055
28	0.229	0.055
29	0.229	0.055
30	0.233	0.055
31	0.233	0.055
32	0.238	0.055
33	0.238	0.055
34	0.250	0.055
35	0.250	0.055
36	0.250	0.055
37	0.250	0.055
38	0.254	0.055
39	0.254	0.055
40	0.271	0.055
41	0.271	0.055
42	0.271	0.055
43	0.271	0.055
44	0.271	0.055
45	0.284	0.055
46	0.284	0.055
47	0.284	0.055
48	0.284	0.055
49	0.284	0.055
50	0.284	0.055
51	0.284	0.055
52	0.284	0.055
53	0.284	0.055
54	0.284	0.055
55	0.284	0.055
56	0.284	0.055
57	0.284	0.055
58	0.284	0.055
59	0.284	0.055
60	1.000	1.000

BIOGRAPHICAL SKETCH

Michael J. Breedlove was born November 28, 1949, in Columbia, Missouri. He attended the University of Missouri–Columbia from 1968 to 1976, earning a Bachelor of Arts (B.A.) degree in geography in 1973 and a Masters of Arts (M.A.) in geography in 1976. For the next 18 years, he held a series of professional research positions with state and local government planning agencies in Missouri, Colorado and Alaska. His professional interests include coastal geomorphology, coral-reef ecosystems and the application of geographic information systems to applied research and education.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Joann Mossa

Joann Mossa, Chairman
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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May, 1999

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